

Physiological Selection ; an Additional Suggestion on the
Origin of Species.

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INTRODUCTION.

THERE can be no one to whom I yield in my veneration for the late Mr. Darwin, or in my appreciation of his work. But for this very reason I feel that in now venturing to adopt in some measure an attitude of criticism towards that work, a few words are needed to show that I have not done so hastily, or without due premeditation.

It is now fifteen years since I became a close student of Darwinism, and during the greater part of that time I have had the privilege of discussing the whole philosophy of Evolution with Mr. Darwin himself. In the result I have found it impossible to entertain a doubt, either upon Evolution as a fact, or upon Natural Selection as a method. But during all these years it has seemed to me that there are certain weak points in the otherwise unassailable defences with which Mr. Darwin has fortified his citadel, or in the evidences with which he has surrounded his theory of natural selection. And the more I have thought upon these points, the greater has seemed the difficulty which they present; until at last I became satisfied that some cause, or causes, must have been at work in the production of species other than that of natural selection, and yet of an equally general kind.

While drifting into this position of scepticism with regard to natural selection as in itself a full explanation of the origin of species, it was to me a satisfaction to find that other evolutionists, including Mr. Darwin himself, were travelling the same way. And since Mr. Darwin's death the tide of opinion continues to flow in this direction; so that at the present time it would be impossible to find any working naturalist who supposes that survival of the fittest is competent to explain all the phenomena of species-formation; while on the side of general reasoning we need not go further than the current issue of the 'Nineteenth Century' to meet with a systematic statement of this view by the highest living authority upon the philosophy of evolution. There-

fore, in now adopting an attitude of criticism towards certain portions of Mr. Darwin's work, I cannot feel that I am turning traitor to the cause of Darwinism. On the contrary, I hope thus to remove certain difficulties in the way of Darwinian teaching; and I well know that Mr. Darwin himself would have been the first to welcome my attempt at suggesting another factor in the formation of species, which, although quite independent of natural selection, is in no way opposed to natural selection, and may therefore be regarded as a factor supplementary to natural selection.

DIFFICULTIES AGAINST NATURAL SELECTION AS A THEORY OF THE ORIGIN OF SPECIES.

The cardinal difficulties in the way of natural selection, considered as a theory of the origin of species, are three in number:—

1st. The difference between natural species and domesticated varieties in respect of fertility.

Mr. Darwin himself allows that this difference cannot be explained by natural selection; and indeed proves very clearly, as well as very candidly, that it must be due to causes hitherto undetected. As we shall presently find, he treats this difficulty at greater length and with more elaboration than any other; but, as we shall also find, entirely fails to overcome it. Now, seeing of how much importance to any theory on the origin of species is the great and general fact of sterility between species, I need not wait to show how heavily we must here discount the theory of natural selection, considered as a theory to explain the transmutation of species.

2nd. Another fact of almost equal generality is that the features, even other than sterility *inter se*, which serve to distinguish allied species, are frequently, if not usually, of a kind with which natural selection can have had nothing whatever to do; for distinctions of specific value frequently have reference to structures which are without any utilitarian significance. It is not until we advance to the more important distinctions between genera, families, and orders that we begin to find, on any large or general scale, unmistakeable evidence of utilitarian meaning.

This difficulty, as I have MS evidence to show, was first perceived by Mr. Darwin himself; it was afterwards presented in a formidable shape by the German palæontologist Bronn, and subsequently by Broca, Nägeli, and sundry lesser writers as regards

both plants and animals. To all these criticisms Darwin replies in the last editions of his works*, with what degree of success I will presently consider.

3rd. The third and last difficulty which I have to mention consists in the swamping influence upon an incipient variety of free intercrossing. This difficulty was first prominently announced in an anonymous essay by the late Professor Fleeming Jenkin of Edinburgh, published in the 'North British Review' for 1867 †. If to this difficulty we add the consideration adduced

* See 'Origin of Species,' ed. 6, pp. 156-157 and 169-176. 'Variation' &c. ii. pp. 211-219. And as to Instincts, 'Mental Evolution in Animals,' pp. 378-379.

† This article is in all respects a highly remarkable one, and, for the space it covers, presents more searching and effective criticism of Mr. Darwin's theory than any other essay with which I am acquainted. With regard to this particular difficulty from the swamping effects of intercrossing, the criticism is especially cogent, and, so far as I know, is the only criticism of importance which Mr. Darwin has not expressly answered. Without reproducing all the numerical calculations wherewith the author sustains this criticism, it will here be enough to quote one of his illustrations:—

"Suppose a white man to have been wrecked on an island inhabited by negroes, and to have established himself in friendly relations with a powerful tribe whose customs he has learnt. Suppose him to possess the physical strength, energy, and ability of a dominant white race, and let the food and climate of the island suit his constitution; grant him every advantage which we can conceive a white to possess over the native; concede that in the struggle for existence his chance of a long life will be much superior to that of the native chiefs. Yet from all these admissions there does not follow the conclusion that after a limited or unlimited number of generations the inhabitants of the island will be white. Our shipwrecked hero would probably become king; he would kill a great many blacks in the struggle for existence; he would have a great many wives and children, while many of his subjects would live and die as bachelors; an insurance company would accept his life at perhaps one tenth of the premium which they would exact from the most favoured of the negroes. Our white's qualities would certainly tend very much to preserve him to a good old age; and yet he would not suffice in any number of generations to turn his subjects' descendants white. It may be said that the white colour is not the cause of the superiority. True; but it may be used simply to bring before the senses the way in which qualities belonging to one individual in a large number must be gradually obliterated. In the first generation there will be some dozens of intelligent young mulattoes, much superior in average intelligence to the negroes. We might expect the throne for some generations to be occupied by a more or less yellow king; but can any one believe that the whole island will gradually acquire a white or even a yellow population, or that the islanders would acquire the energy, courage, ingenuity, patience, self-control, endurance, in virtue of which qualities our hero killed so many of their

by this author, and afterwards in a more elaborate form by Professor Mivart, as to the improbability of a variation being from the first of sufficient utility to come under the influence of natural selection, I feel it impossible to doubt that a most formidable opposition is presented. For even if, for the sake of argument, we waive Professor Mivart's objection as to the probable inutility of many incipient variations which afterwards, or in a higher degree of perfection, begin to become useful, even if we waive this objection and assume that all useful variations are useful from the first moment of variation, still we have to meet the difficulty from the swamping effects of free intercrossing on the incipient variation, however useful.

Here then we have three great obstructions in the road of natural selection, considered as an explanation of the origin of species. For the sake of brevity I will hereafter allude to these difficulties as those relating to sterility, to inutility, and to intercrossing. Let us now consider how these difficulties have been dealt with in the later editions of Mr. Darwin's works.

STERILITY BETWEEN SPECIES.

Founding his argument for natural selection upon the basis furnished by the known effects of artificial selection, Mr. Darwin had to meet the question why it is that the supposed products of the former differ from the known products of the latter in being so much more sterile *inter se*; or, in other words, why it is that natural species differ so conspicuously from artificial varieties in respect of mutual fertility. In order to meet this question, Mr. Darwin adduced a variety of considerations, each of which he substantiated by so large an accumulation of facts, that, as I have already observed, his discussion of the question as a whole is one of the most laboured portions of all his laborious work. From which we may perceive how fully Mr. Darwin recognized the formidable nature of this difficulty. I will now summarize the considerations whereby he sought to overcome it. And this I can do most briefly by arranging them in an order of my own.

ancestors, and begot so many children; those qualities, in fact, which the struggle for existence would select, if it could select anything?

"Here is a case in which a variety was introduced with far greater advantages than any sport ever heard of, advantages tending to its preservation, and yet powerless to perpetuate the new variety."

In the first place, differences of type in nature are by naturalists classified as differences of species, principally because they are found to be mutually sterile. Thus it is but circular reasoning to argue that all natural species are shown by nature herself to differ from artificial varieties in presenting this peculiarity of mutual sterility; for it is mainly in virtue of presenting this peculiarity that they have been classified as species. The real question, therefore, that stands to be considered is simply this: Why should the modifications of organic types supposed to have been produced by natural selection have so frequently and generally led to mutual sterility, when even greater modifications of such types known to have been produced by artificial selection continue to be mutually fertile?

In the next place, the distinction in question is not absolute. On the one hand, some few domesticated varieties, when crossed with one another, exhibit a more or less marked degree of sterility; and, on the other hand, a large number of wild species, when crossed with one another, exhibit fertility, and this in all degrees. So that the distinction between natural species and artificial varieties in respect of fertility is, as a matter of fact, not absolute, but breaks down in both its parts.

Nevertheless, although this distinction is not absolute, it is undoubtedly, and as a general rule, valid. That is to say, it is unusual or exceptional to find complete fertility between natural species, and it is still more so to find even partial sterility between artificial varieties. Therefore, notwithstanding his success in showing that there is no absolute distinction between species and varieties in this respect, Mr. Darwin plainly perceived that there still remained a relative distinction of a most general and important kind. In order to mitigate the severity of this distinction, he furnished elaborate proof of the following facts.

1st. That with natural species the cause of sterility lies exclusively in differences of the sexual system.

2nd. That the conditions of life which occur under domestication tend to enhance fertility, and this to such an extent as to render the domesticated descendants of mutually sterile species mutually fertile, as in the case of our domesticated dogs.

Now, these two facts undoubtedly help to explain why the great changes of organic types produced by artificial selection have not resulted in superinducing mutual sterility; but they do not appear to throw any light at all on the question, why it is

that smaller changes of organic type, when produced by natural selection and now known as species, should so generally be attended with this result? Or, as Mr. Darwin himself expresses it, "the real difficulty in our present subject is not, as it appears to me, why domestic varieties have not become mutually infertile when crossed, but why this has so generally occurred with natural varieties, as soon as they have been permanently modified in a sufficient degree to take rank as species."

Here, then, we have the core of the problem; and it is just here that Mr. Darwin's explanations fail. For he candidly says, "We are far from precisely knowing the cause;" and the only suggestion he adduces to account for the fact is, that varieties occurring under nature "will have been exposed during long periods of time to more uniform conditions than have domesticated varieties; and this may well make a wide difference in the result." I need scarcely wait to show the feebleness of this suggestion. When we remember the incalculable number of animal and vegetable species, living and extinct, we immediately feel the necessity for some much more general explanation of their existence than is furnished by supposing that their mutual sterility, which constitutes their most general or constant distinction, was in every case due to some incidental effect produced on the generative system by uniform conditions of life. To say nothing of the antecedent improbability, that in all these millions and millions of cases the reproductive system should happen to have been affected in this peculiar way by the merely negative condition of uniformity, there is, as it seems to me, the overwhelming consideration that, at the time when a variety is first forming, this condition of prolonged exposure to uniform conditions of life must necessarily be absent as regards that variety; yet this is just the time when we must suppose that the infertility with its parent form arose. For, if not, the incipient variety would at once have been re-absorbed into the parent form by intercrossing, as we shall see more fully under the next head of this criticism.

In view of these considerations I conclude, that while Mr. Darwin has given the best of reasons to show why domesticated varieties have so rarely become sterile *inter se*, he has entirely failed to suggest any reason why this should so generally have been the case with natural species.

SWAMPING EFFECTS OF INTERCROSSING.

On this subject Mr. Darwin writes, "Most animals and plants keep to their proper homes, and do not needlessly wander about; we see this with migratory birds, which almost always return to the same spot. Consequently, each newly-formed variety would generally be at first local, as seems to be the common rule with varieties in a state of nature; so that similarly modified individuals would soon exist in a small body together, and would often breed together. If the new variety were successful in its battle for life, it would slowly spread from a central district, competing with and conquering the unchanged individuals on the margin of an ever-increasing circle."*

Now, to my mind, these considerations do not dispose of the difficulty in question. In the first place, a very large assumption is made when the newly-formed variety is spoken of as represented by "similarly modified individuals"—the assumption, namely, that the same variation occurs simultaneously in a number of individuals inhabiting the same area. Of course, if this assumption were granted, there would be an end of the present difficulty; for if a sufficient number of individuals were thus simultaneously and similarly modified, there need be no longer any danger of the variety becoming swamped by intercrossing. But the force of the difficulty consists in the very fact of this assumption being required to meet it. The theory of natural selection, as such, furnishes no warrant for supposing that the same beneficial variety should arise in a number of individuals simultaneously. On the contrary, the theory of natural selection trusts to the chapter of accidents in the matter of variation; and in this chapter we read of no reasons why the same beneficial variation should arise simultaneously in a sufficient number of individual cases to prevent its being swamped by intercrossing with the parent form. Or, to state the case in other words, in whatever measure the assumption in question is resorted to, in that measure is the theory of natural selection confessed inadequate to furnish an explanation of the origin of species. And to this must be added the important consideration already adduced, namely, that a very large proportion, if not the majority, of features which serve to distinguish species from species are features presenting no utilitarian significance; and

* 'Origin of Species,' ed. 6, pp. 72-3 *et seq.*

therefore that, even if they were each conceded to have arisen in a number of individuals simultaneously, they would not have benefited those individuals in their struggle for existence with the parent form. Hence their re-absorption by intercrossing would not be hindered by natural selection, which is the agency here invoked by Mr. Darwin to account for their continuance. This consideration, however, introduces us to the third and last of the difficulties with which the theory of natural selection is beset.

INUTILITY OF SPECIFIC CHARACTERS.

The only answer which Mr. Darwin makes to this difficulty is, that structures and instincts which appear to us useless may nevertheless be useful. But this seems to me a wholly inadequate answer. Although in many cases it may be true, as indeed it is shown to be by a number of selected illustrations furnished by Mr. Darwin, still it is impossible to believe that it is always, or even generally so. In other words, it is impossible to believe that in all, or even in most, cases where minute specific differences of structure or of instinct are to all appearance useless, they are nevertheless useful. Observe, the case would be different if the great majority of specific distinctions, like the great majority of larger distinctions, were of obvious utilitarian significance. In this case we might reasonably set down the exceptions as proof of the rule, or hold that they appear to be exceptions only on account of our ignorance. But it is certainly too large a demand upon our faith in natural selection to appeal to the argument from ignorance, when the facts require that this appeal should be made over so very large a number of instances. We might, for example, most reasonably conclude that the callosities on the hind legs of horses, or the instinct of covering their excrement shown by certain roaming Carnivora, are of some such hidden use to the animals as to have preserved them in their struggle for existence. I say, we might reasonably conclude this, provided that such instances were exceptional. But seeing that so enormous a number of specific peculiarities are in the same predicament, it surely becomes the reverse of reasonable so to pin our faith to natural selection as to conclude that all these peculiarities must be useful, whether or not we can perceive their utility. For by doing this we are but reasoning in a circle. The only evidence we have of natural selection is furnished by the observed utility

of innumerable structures and instincts which for the most part are of generic, family, or higher order of taxonomic value. Therefore, unless we reason in a circle, it is not competent to argue that the apparently useless structures and instincts of specific value are due to some kind of utility which we are unable to perceive. But I need not argue this point, because in the later editions of his works Mr. Darwin freely acknowledges that a large proportion of specific distinctions must be conceded to be useless to the species presenting them; and, therefore, that they resemble the great and general distinction of mutual sterility in not admitting of any explanation by the theory of natural selection.

NATURAL SELECTION NOT A THEORY OF THE ORIGIN OF SPECIES.

In view of the foregoing considerations it appears to me obvious that the theory of natural selection has been misnamed; it is not, strictly speaking, a theory of the origin of *species*: it is a theory of the origin—or rather of the cumulative development—of *adaptations*, whether these be morphological, physiological, or psychological, and whether they occur in species only, or likewise in genera, families, orders, and classes. These two things are very far from being the same; for, on the one hand, in an enormously preponderating number of instances, adaptive structures are common to numerous species; while, on the other hand, the features which serve to distinguish species from species are, as we have just seen, by no means invariably—or even generally—of any adaptive character. Of course, if this were not so, or if species always and only differed from one another in respect of features presenting some utility, then any theory of the origin of such adaptive features would also become a theory of the origin of the species which present them. As the case actually stands, however, not only are specific distinctions very often of no utilitarian meaning; but, as already pointed out, the most constant of all such distinctions is that of sterility, and this the theory of natural selection is confessedly unable to explain.

For these reasons I think there can be no doubt that the theory of natural selection ought to be recognized as exclusively a theory of the evolution of adaptive modifications; not therefore or necessarily a theory of the evolution of different species. And, if once this important distinction is clearly perceived, the

theory in question is released from all the difficulties which we have been considering. For these difficulties have beset the theory only because it has been made to pose as a theory of the origin of species; whereas, in point of fact, it is nothing of the kind. In so far as natural selection has had anything to do with the genesis of species, its operation has been, so to speak, incidental; it has only helped in the work of originating species in so far as some among the adaptive variations which it has preserved happen to have constituted differences of only specific value. But there is an innumerable multitude of other such differences with which natural selection can have had nothing to do—particularly the most general of all such differences, or that of mutual sterility—while, on the other hand, by far the larger number of adaptations which it has preserved are now the common property of numberless species. Let it, therefore, be clearly understood that it is the office of natural selection to evolve adaptations—not therefore or necessarily to evolve species. Let it also be clearly understood that in thus seeking to place the theory of natural selection on its true logical footing, I am in no wise detracting from the importance of that theory. On the contrary, I am but seeking to release it from the difficulties with which it has been hitherto illegitimately surrounded*.

Again, it is comparatively seldom that we encounter any difficulty in perceiving the utilitarian significance of generic and family distinctions, while we still more rarely encounter any such difficulty in the case of ordinal and class distinctions. Why, then, should we so often encounter this difficulty in the

* It will be at once apparent how this release is effected. For, if it be clearly recognized that natural selection has to do with the evolution of species only in so far as specific distinctions happen to be of utilitarian character, all objections to the theory raised from its inability to explain the whole origin of species (or the general fact of sterility between allied species, and the frequently non-utilitarian character of specific distinctions) become irrelevant; whatever its professions may have been, in point of fact the theory has nothing to do with explaining any of these things, and, therefore, ought never to have been held responsible for their explanation. Again, as regards the difficulty from the overwhelming effects of intercrossing, this really concerns the theory of natural selection only in the case of varieties; not in that of species, genera, families, &c. Yet the work of natural selection in maintaining and perfecting adaptive structures in these higher taxonomic divisions is probably of quite as much importance as its work in seizing upon the earliest beneficial variations, although this fact has been lost sight of in the eagerness of naturalists to constitute the theory an explanation of the origin of species.

case of specific distinctions? Surely because some cause other than natural selection must have been at work in the differentiation of species, which has operated in a lesser degree in the differentiation of genera, and probably not at all in the differentiation of families, orders, and classes. Such a cause it is the object of the present paper to suggest; and if in the foregoing preamble it appears somewhat presumptuous to have insinuated that Mr. Darwin's great work on the 'Origin of Species' has been misnamed, I will conclude the preamble with a quotation from that work itself, which appears at once to justify the insinuation, and to concede all that I require.

"Thus, as I am inclined to believe, morphological differences, which we consider as important, such as the arrangement of the leaves, the division of the flower or of the ovary, the position of the ovules, &c., first appeared in many cases as fluctuating variations, which sooner or later became constant through the nature of the organism and of the surrounding conditions, as well as through the intercrossing of distinct individuals; but not through natural selection; for as these morphological characters do not affect the welfare of the species, any slight variations in them could not have been governed or accumulated through this latter agency. It is a strange result which we thus arrive at, namely that characters of slight vital importance to the species are the most important to the systematist"*.

* 'Origin of Species,' ed. 6, p. 176. See also p. 365 *et seq.* The argument is that the guiding principle of classification being a hitherto unconscious tracing of the lines of genetic descent, and heredity not being more concerned with preserving useful variations than indifferent ancestral peculiarities, the latter are now of more use than the former to systematists, seeing that they have been allowed to persist without undergoing adaptive modification at the hands of natural selection. I have no doubt that this argument is sound; but the "strange result" to which it leads implies that natural selection has throughout been the cause of the origin of adaptations; not therefore necessarily, or even generally, of the origin of species. But let me not be misunderstood. In saying that the theory of natural selection is not, properly speaking, a theory of the origin of species, I do not mean to say that the theory has no part at all in explaining such origin. Any such statement would be in the last degree absurd. What I mean to say is that the theory is one which explains the origin or the conservation of adaptations, whether structural or instinctive, and whether these occur in species, genera, families, orders, or classes. In so far, therefore, as useful structures are likewise species-distinguishing structures, so far is the theory of their origin also a theory of the origin of the species which present them. But useful structures and species-distinguishing struc-

EVOLUTION OF SPECIES BY INDEPENDENT VARIATION.

Enough has now been said to justify the view that there must be some cause or causes, other than natural selection, operating in the evolution of species. And this is no more than Mr. Darwin himself has expressly and repeatedly stated to have been his own view of the matter; nor am I aware that any of his followers have thought otherwise. Hitherto the only additional causes of any importance that have been assigned are use and disuse, sexual selection, correlated variability, and yet another principle which I believe to have been of much more importance than any of these—not even excepting the first, where the origin of species only is concerned. Yet it has attracted so little attention as scarcely ever to be noticed by writers on Evolution, and never even to have received a name. For the sake of convenience, therefore, I will call this principle the Prevention of Intercrossing with Parent Forms, or the Evolution of Species by Independent Variation.

First, let us consider how enormous must be the number of variations presented by every generation of every species. According to the Darwinian theory, it is only those variations which happen to have been useful that have been preserved; yet, even as thus limited, the principle of variability is held to have been sufficient to furnish material out of which to construct the whole adaptive morphology of nature. How immense, therefore, must be the number of unuseful variations. These are probably many hundred of times more numerous than the useful variations, although they are all, as it were, stillborn, or allowed to die out immediately by intercrossing. Hence, as a matter of fact, we find that no one individual “is like another all in all;” which is another way of saying that a specific type may be regarded as

tures are very far from being convertible terms. On the one hand, as we have seen, many useful structures are shared by many species in common; and, on the other hand, many species-distinguishing structures are not useful. Therefore I say that the theory which explains the origin of useful structures is not, strictly speaking, a theory of the origin of species; it only explains the origin of species in cases where it happens that one species differs from another in respect of features all of which present utilitarian significance. And this, as even Mr. Darwin himself allows, is very far from being universally, or even usually, the case.

the average mean of all individual variations, any considerable departure from this average being, however, checked by intercrossing.

But now, should intercrossing by any means be prevented, there is no reason why unuseful variations should not be perpetuated by heredity quite as well as useful ones when under the nursing influence of natural selection—as, indeed, we see to be the case in our domesticated productions. Consequently, if from any cause a section of a species is prevented from intercrossing with the rest of its species, we might expect that new varieties—for the most part of a trivial and unuseful kind—should arise within that section, and that in time these varieties should pass into new species. And this is just what we do find. Oceanic islands, for example, are well known to be extraordinarily rich in peculiar species; and this can best be explained by considering that a complete separation of the fauna and flora on such an area permits them to develop independent histories of their own, without interference by intercrossing with their original parent forms. We see the same principle exemplified by the influence of geographical barriers of any kind, and also by the consequences of migration. For when a species begins to disperse in different directions from its original home, those members of it which constitute the vanguard of each advancing army are much more likely to perpetuate any individual variations that may arise among them, than are the members which still occupy the original home. Not only is the population much less dense on the outskirts of the area occupied by the advance guard; but beyond these outskirts there lies a wholly unoccupied territory upon which the new variety may gain a footing during the progress of its further migration. Thus, instead of being met on all sides by the swamping effects of intercrossing with its parent form, the new variety is now free to perpetuate itself with comparatively little risk of any such immediate extinction. And the result is that wherever we meet with a chain of nearly allied specific forms so distributed as to be suggestive of migration with continuous modification, the points of specific difference are trivial or non-utilitarian in character. Clearly this general fact is in itself enough to prove that, given an absence of overwhelming intercrossing, independent variability may be trusted to evolve new species. The evidence which I have collected, and

am collecting, of this general fact must be left to constitute the subject of a future publication*.

PHYSIOLOGICAL SELECTION, OR SEGREGATION OF THE FIT.

Were it not for the very general occurrence of some degree of sterility between allied species, and were it not also for the fact that closely allied species are not always, or even generally, separated from one another by geographical barriers †, one might reasonably be disposed to attribute all cases of species-formation by independent variability to the prevention of intercrossing by geographical barriers, and by migration. But it is evident that these two facts can no more be explained by the influence of geographical barriers, or by migration, than they can be by the influence of natural selection. It is therefore the object of the present paper to suggest an additional factor in the formation of specific types by independent variability, and one which appears to me fully competent to explain both the general facts just mentioned.

Of all parts of those variable beings which we call organisms, the most variable is the reproductive system. It is needless for me to remind any reader of Mr. Darwin's works what a mass of evidence he has accumulated, showing the extreme sensitiveness of the reproductive system to small changes in the conditions of life.

The consequent variations may occur either in the direction of increased fertility, as with our domesticated varieties, or in that of sterility in all degrees, as with wild species when confined. So extreme is the sensitiveness of the reproductive system in these respects—or, in other words, so liable is this system to vary—

* So far as I am aware, the first writer who insisted on the great importance of the prevention of intercrossing in the evolution of species, both by isolation and migration, was Moritz Wagner. Since then Wallace, Weismann, and others, as also Darwin himself, have in lesser degrees recognized this factor. The most recent contribution to the subject is by a Fellow of this Society, Mr. Charles Dixon, whose work on 'Evolution without Natural Selection' presents a large and admirable body of facts, showing the important part which the prevention of intercrossing has played in the evolution of species among Birds. But I cannot find that any previous writer has alluded to the principle which it is the object of the present paper to enunciate, and which is explained in the succeeding paragraphs.

† As Mr. Wallace observes, allied species usually occupy contiguous areas, which more often than not are likewise continuous.

that in many cases, even when tamed in their own countries, allowed freedom, fed on their natural food, and so forth, animals become absolutely sterile. Moreover, so delicately is the reproductive system balanced in respect of variability, that sometimes it will change in the direction of sterility and sometimes in the opposite direction of increased fertility, under a change of conditions the same in kind, but different in degree. Lastly, in numberless individual cases variability occurs in either of these two opposite directions without any assignable reason at all, or, in Mr. Darwin's language, spontaneously. So that, on the whole, we must accept it as a fact that the reproductive system, both in plants and animals, is preeminently liable to vary, and this both in the direction of sterility and in that of increased fertility. Indeed, Mr. Darwin goes so far as to say: "It would appear that any change in the habits of life, whatever these habits may be, if great enough, tends to affect, in an inexplicable manner, the powers of reproduction." And he adds this important qualification: "The result depends more on the constitution of the species than on the nature of the change; for certain whole groups are affected more than others; but exceptions always occur, for some species in the most fertile groups refuse to breed, and some in the most sterile groups breed freely."

Now, having regard to all these delicate, complex, and for the most part hidden conditions which determine this double kind of variation within the limits of the reproductive system, there can be no difficulty in granting that variations in the direction of greater or less sterility must frequently occur in wild species. Probably, indeed, if we had any means of observing this point, we should find that there is no one variation more common; but of course, whenever it arises, whether as a result of changed conditions of life, or, as we say, spontaneously, it immediately becomes extinguished, seeing that the individuals which it affects are less able, if able at all, to propagate the variation; or, if the variation should extend to all the individuals of a species under a change of environment, that the species would become extinct.

Let these three points, then, be clearly kept in mind: 1st, that when a section of any species is cut off by geographical barriers, or by migration, from intercrossing with its parent form, it tends to run into new varieties, and so eventually to develop new

species ; 2nd, that the number of un-useful variations taking place in all species is incalculable ; and 3rd, that the reproductive system is so especially variable, both intrinsically and in response to changed conditions of life, that increase of sterility must often arise as a variation under nature.

I have now fully, if not tediously, prepared the way for explaining the suggestion which I have to make. From what has been said it may be concluded that all the multitude of individual variations perpetually occurring in every species become re-absorbed in the specific type by intercrossing, unless the variations happen to be either useful, to take place in isolation, or by way of what Mr. Spencer calls "direct equilibration," such as use, disuse, and so forth. It has also been shown that any variations in the reproductive system which take place in the direction of increased sterility must likewise tend to become extinguished. But now it must be added that there is one such variation in the reproductive system to which this remark does not apply. For if the variation be such that the reproductive system, while showing some degree of sterility with the parent form, continues to be fertile within the limits of the varietal form, in this case the variation would neither be swamped by intercrossing, nor would it die out on account of sterility. On the contrary, the variation would be perpetuated with more certainty than could a variation of any other kind. For, in virtue of increased sterility with the parent form, the variation would not be exposed to extinction by intercrossing ; while, in virtue of continued fertility within the varietal form, the variation would perpetuate itself by heredity, just as in the case of variations generally when not re-absorbed by intercrossing. To make my meaning perfectly clear I will use an illustration.

Suppose the variation in the reproductive system is such that the season of flowering or of pairing becomes either advanced or retarded. Whether this variation be, as we say, spontaneous, or due to any change of food, habitat, climate, etc., does not signify. The only point we need here attend to is that some individuals, living on the same geographical area as the rest of their species, have varied in their reproductive systems, so that they can only propagate with each other. They are thus perfectly fertile *inter se*, while absolutely sterile with all the other members of their species. This particular variation being communicated by inheritance to their progeny, there would soon arise on the same area,

or, if we like, on closely contiguous areas, two varieties of the same species, each perfectly fertile within its own limits, while absolutely sterile with one another. That is to say, there has arisen between these two varieties a barrier to intercrossing which is quite as effectual as a thousand miles of ocean; the only difference is that the barrier, instead of being geographical, is physiological.

Now, from this illustration I hope it will be obvious that wherever any variation in the highly variable reproductive system occurs, tending to sterility with the parent form while not impairing fertility with the varietal form—no matter whether this is due, as here supposed, to a slight change in the season of reproductive activity, or to any other cause—there the physiological barrier in question must interpose, with the result of dividing the species into two parts. And it will be further evident that when such a division is effected, the same conditions are furnished to the origination of new species as are furnished to any part of a species when separated from the rest by geographical barriers. For now the two physiologically divided sections of the species are free to develop independent histories without mutual intercrossing.

Or, to state this suggestion in another way. If the suggestion is well founded, it enables us to regard a large proportion, if not the majority, of natural species as so many expressions of variation in the reproductive systems of their ancestors. When accidental variations of a non-useful kind occur in any of the other systems or parts of an organism, they are, as a rule, immediately extinguished by intercrossing. But whenever they happen to arise in the reproductive system in the way here suggested, they must inevitably tend to be preserved as new natural varieties or incipient species. Once formed as such, the new natural variety, even though living upon the same area as its parent species, will begin an independent course of history; and, as in the now analogous case of isolated varieties, will tend to increase its morphological distance from the parent form, until it eventually becomes a true species. At least it appears to me obvious that in so many cases as variations of the kind in question have taken place, in so many cases must the conditions have been supplied to the formation of new species. Later on I will show in more detail how these conditions have been utilized.

The principle thus briefly sketched in some respects resembles and in other respects differs from the principle of natural selection, or survival of the fittest. For the sake of convenience, therefore, and in order to preserve analogies with already existing terms, I will call this principle Physiological Selection, or Segregation of the Fit.

ARGUMENTS À PRIORI.

Before stating the evidence which I have been able to collect of the operation of this principle, it is desirable that I should make one or two general remarks upon the conditions under which alone this evidence can be presented.

First, let it be observed that if this particular kind of variation ever takes place at all, we are not concerned either with its causes or with its degrees. Not with its causes, because in this respect the theory of physiological selection is in just the same position as that of natural selection; it is enough for both that the needful variations are provided, without it being incumbent on either to explain the causes which underlie the variations. Nor is the theory of physiological selection concerned with the degrees of sterility which may in any particular cases have been initially supplied. For, whether the degree of sterility with the parent form is originally great or small, the result of it in the long run will be the same; the only difference will be that in the latter case a greater number of generations would be required in order to separate the varietal from the parent form, as a little thought will be enough to show*.

Next, let it be observed that, from the nature of the case, we cannot expect to meet with much direct evidence of physiological selection yielded by our domesticated varieties. For, first, it has never been the object of breeders or horticulturists to go back to the wild stocks, and therefore observations on this point are wanting; second, breeders and horticulturists keep their strains separate, and many kinds of variation are preserved other than those

* Suppose that, on an average, a cross between the parent and the variety were to yield a progeny of 2, while a cross between two individuals of the new variety were to yield a progeny of 3. In this case there is but a very small degree of sterility towards the parent form; yet if figured out it will be found—supposing this degree of sterility to be inherited by the pure-bred varieties—abundantly sufficient to ensure multiplication of the varietal type, without danger of this type being swamped by the parental.

of the reproductive system with which alone we are concerned, and which must be extremely rare as compared with all the other kinds of variation that it is the aim of breeders and horticulturists to preserve ; for, third, it is never the aim of these men to preserve this particular kind of variation. In view of these three considerations, it is clear that we cannot expect to derive much evidence of physiological selection from our domesticated varieties, further than the general proof which these afford of the primary importance of preventing intercrossing with parent forms, if a new varietal form is ever to gain a footing. No one of these domesticated varieties could have been what it now is, unless such intercrossing had been systematically prevented by man ; and this gives us good reason to infer that no natural species could have been what it now is, unless every variety in which every species originated had been prevented from intercrossing with its parent form by nature. For we have seen that even if the initial variation, which, as a matter of fact, was in each case preserved, happened to have been useful—and this supposition is, as we have also seen, the reverse of true—it would still be so eminently liable to extinction by intercrossing, that it is at least doubtful whether its preservation could have been secured by natural selection alone. Hence, although we cannot obtain much direct evidence in favour of physiological selection from plants and animals under domestication, we do obtain from them such indirect evidence as arises from proof of the importance of preventing intercrossing with parent forms.

Again, as to plants and animals under nature, the particular variation with which alone we are concerned would probably not be noticed until it had given rise to a new species. In this respect, therefore, the theory of physiological selection is in the same predicament as that of natural selection ; in neither case are we able directly to observe the formation of one species out of another by the agency supposed ; and therefore in both cases our belief in the agency supposed must, to a large extent, depend on the probability established by general considerations. Nevertheless, although our sources of direct evidence are thus seen to be necessarily limited, I shall now hope to show that they are sufficient to prove the only fact which they are required to prove, namely, that the particular kind of variation which is in question does occur, both in nature and under domestication.

Although, as above remarked, the theory of physiological

selection is not necessarily concerned with the causes of variation in the reproductive system, it will be convenient to classify these causes as extrinsic and intrinsic. By the extrinsic causes I mean changes in the environment which act upon the reproductive system, whether these be changes of food, climate, degree of liberty, and so forth. By intrinsic causes I mean changes taking place in the reproductive system itself of a kind depending on what Mr. Darwin calls "the nature of the organism," or on causes which we are not able to trace, and which may therefore be termed spontaneous.

Now the particular kind of variation the occurrence of which I have to prove is that of impotency—whether absolute or comparative—towards the parent form, without decrease of potency towards the varietal form. One very obvious example of this kind of variation has already been given in the season of flowering or of pairing being either advanced or retarded. This I conceive to be a most important case for us, inasmuch as it is one that must frequently arise in nature. Depending, as it chiefly does, on external causes, numberless species both of plants and animals must, I believe, have been segregated by its influence. For in every case where a change of food, temperature, humidity, altitude, or of any of the other many and complex conditions which go to constitute environment—whether the change be due to migration of the species, or to alterations going on in an area occupied by a stationary species—in every case where such a change either promotes or retards the season of propagation, there we have the kind of variation which is required for physiological selection. And it is needless to give detailed instances of its occurrence where this is due to so well-known and frequently-observed a cause.

But it is in what I have called the spontaneous variability of the reproductive system itself that I mainly rely for evidence of physiological selection. The causes of variability are here far more numerous, subtle, and complex than are such extrinsic causes as those above mentioned; and they are always at work in the reproductive systems of all organisms. Moreover, sensitive as the reproductive system is to small changes in the conditions of life, its spontaneous variability is, as Mr. Darwin has shown, even more remarkable. Now, among all the possible variations of the reproductive system however caused, there is one which, whenever it is produced, cannot be allowed again to disappear;

but must be perpetuated by the ever vigilant agency of physiological selection. What this particular variation is we now know, and I will proceed to give evidence of its spontaneous occurrence, first in individuals, second in varieties, and third in species.

1. *Individuals*.—Mr. Darwin observes:—"It is by no means rare to find certain males and females which will not breed together, though both are known to be perfectly fertile with other males and females. We have no reason to suppose that this is caused by these animals having been subject to any change in their habits of life; therefore such cases are hardly related to our present subject. The cause apparently lies in an innate sexual incompatibility of the pair when matched." He then proceeds to give examples from horses, cattle, pigs, dogs, and pigeons, concluding with the remark that "these facts are worth recording, as they show, like so many previous facts, on what slight constitutional differences the fertility of an animal often depends"*. And in another place he gives references to similar facts in the case of plants †.

Now, if it were needful, I could supply a number of additional cases of this individual incompatibility, or of absolute sterility as between two individuals, each of which is perfectly fertile with all other individuals ‡. But I think that the not unusual occurrence of this fact will be regarded as abundantly substantiated by these references.

And here, it appears to me, we have a most significant piece of evidence upon the origin of species. If even as between two individuals there may thus arise absolute sterility, without there being in either of them the least impairment of fertility with other individuals, is it not obvious that we have precisely the kind of variation which my theory requires, and that we have this variation spontaneously or suddenly given in the highest possible degree of efficiency? Shallow criticism might reply that this is the precise opposite of the variation which my theory requires; and under one point of view such is the case. For here we have

* 'Variation,' &c., vol. ii. pp. 145-6. † 'Origin of Species,' ed. 6, p. 246.

‡ I may remark that individual incompatibility is especially apt to declare itself when the individuals paired belong to different species. That is to say, while some individuals taken from the two species will readily produce hybrids, other individuals taken from the same species will prove hopelessly sterile. The same applies to the fertility of hybrids. These facts are of some additional importance to us, because they occupy a kind of intermediate position between these given above and those given in the next succeeding paragraphs.

sterility towards the varietal form, with unimpaired fertility towards the parent form. But a little thought will show that this criticism would be shallow. The important fact is that among a number of individuals of the same species, all exposed to apparently the same conditions of life, some of the number so far deviate from the specific type in respect of their reproductive systems as to be absolutely sterile with certain members of their own species, while remaining perfectly fertile with other members. In terms of the above criticism, therefore, this fact might be translated into saying that if the reproductive system can be proved to undergo so remarkable a variation as that of *individual* incompatibility, much more is it likely to undergo the "opposite" variation, wherein a similar incompatibility would extend to a larger number of individuals. For certainly the most remarkable feature about this individual incompatibility is the fact of its being only individual. It would not be nearly so remarkable, or physiologically improbable, that such incompatibility should run through a whole race or strain. Therefore, the fact of individual incompatibility appears to me to furnish most important evidence of my theory; for it proves that even the most apparently capricious and wholly unaccountable variations may spontaneously arise within the limits of the reproductive system—variations which, physiologically considered, are much more remarkable, or antecedently improbable, than anything that my theory requires.

2. *Races*.—But of even more importance to us is the direct evidence of such a state of matters in the case of varieties, breeds, or strains. Incompatibility between individuals is, indeed, of very great importance to my theory, because it constitutes the first link in a chain of direct evidence as to the actual occurrence of the particular kind of variation on which the theory depends; here we have, as it were, the first beginning in an individual organism of a change which, under suitable conditions, may give rise to a new strain, and so eventually to a new species. But, seeing that the individual is so small a constituent part of his species, unless his peculiar incompatibility has reference to the majority of other individuals, so that it becomes only the minority of the opposite sex with whom he can pair, the probability is that the peculiar condition of his reproductive system would not be perpetuated by heredity, but would become extinguished by intercrossing. As I have already said, it is, physiologically considered, even more remarkable that such

incompatibility should ever be exclusively individual than that it should be racial; and therefore, as likewise remarked, I regard these cases of individual incompatibility as of value to my theory chiefly because they prove the actual occurrence of the variation which the theory requires, and this as suddenly or spontaneously arising in the highest degree of efficiency. But I will now adduce evidence to show that a state of matters more or less similar may be proved to obtain throughout a whole breed or strain, so that we then have, not merely individual incompatibility, but what may be termed racial incompatibility; and therefore that we are on the highroad to the branching-place of a new species. Here I will again quote my facts from Darwin, partly because he has so profoundly studied the subject of variation, but chiefly because, wherever it is possible, I desire to rely upon his authority.

In the ninth chapter of the 'Origin of Species,' and in the nineteenth chapter of the 'Variation of Plants and Animals under Domestication,' Mr. Darwin adduces miscellaneous evidence of the fact that in many cases varieties of the same species exhibit a higher degree of fertility within themselves than they do with one another. In this respect, therefore, they resemble natural species. Inasmuch, however, as they are not natural species, but domesticated varieties (or the changed descendants of one natural species), they are here available as evidence to prove what I have just called racial incompatibility, due to the change which has been effected in their reproductive systems. It makes no difference whether we regard this change as due to intrinsic or to extrinsic causes; in either case the racial incompatibility is the same, and this is all that the theory of physiological selection requires. Take, for example, the following case which, as Mr. Darwin says, "is the result of an astonishing number of experiments made during many years on nine species of *Verbascum*, by so good an observer and so hostile* a witness as Gärtner: namely, that the yellow and white varieties when crossed produce less seed than the similarly coloured varieties of the same species;" and elsewhere he quotes a statement from the same authority to the effect that the blue and red varieties of the pimpernel are absolutely sterile together, while each is perfectly fertile within itself. So that in these cases we have a marked degree of racial incompatibility between

* "Hostile" because Gärtner believed that the distinction between species and varieties in respect of sterility is more absolute than Darwin believed.

yellow and white varieties, or between blue and red varieties of the same species, while each continues fertile within its own limits. And similarly in all the other cases.

Now, in these facts one may only see evidence of changes in the organism reacting on the reproductive system in such a way as to produce this particular effect. I shall have more to say on this subject later on; here it is enough to remark that it matters little to my theory whether the changes be thus due to reaction on the reproductive system, or have arisen in the reproductive system, as it were, independently; for, as above observed, whether the causes of the change be supposed intrinsic or extrinsic, the change itself is really all that we are now concerned with. This change, however produced, is a change in the direction of what I call racial incompatibility, and therefore, if it had taken place in any wild species, must necessarily have constituted a physiological barrier to intercrossing between the two varieties, which, according to my theory, is the primary condition required for the development of varieties into species. And that such a state of matters is at least as likely to occur in a wild species as in a domesticated descendant is obvious. For domestication, as a rule, increases fertility, and therefore is, as a rule, inimical to sterility, sometimes even breaking down the physiological barriers between natural species. Therefore, if at other times even under domestication the reproductive system may vary so as to erect these barriers between artificial varieties, much more are such barriers likely to be erected between varieties when these arise in a state of nature. Indeed, the difficulty is to find such cases in a state of domestication, the great difference between mongrels and hybrids consisting in this very fact of the former being so usually fertile, and the latter so usually sterile. But I trust that enough has now been said to show that even among our domestic productions we may find evidence of racial incompatibility, or of that particular variation in the reproductive apparatus which is required by the theory of physiological selection.

As regards varieties in a state of nature, it must be noticed, first of all, that racial incompatibility is not likely to be observed. For, on the one hand, if such incompatibility is in any degree pronounced, for this very reason the two forms would be ranked by naturalists as distinct species; while, on the other hand, if not so pronounced, the fact of incompatibility could only be revealed by careful observation. For these reasons the evidence which I

have to give of incompatibility in a state of nature is derived chiefly from species, as I will now explain.

3. *Species*.—According to the general theory of evolution, which in this paper is taken for granted, the distinction between varieties and species is only a distinction of degree; and the distinction is mainly, as well as most generally, that of mutual sterility, whether absolute or partial. Therefore I am here supplied with an incalculable number of instances, all tending to support my theory; for in so many instances as variation has led to any degree of sterility between parent and varietal forms, or between the varying descendants of the same form, in so many instances it is a simple statement of fact to say that physiological selection must have taken place. There remains, however, the question whether the particular change in the reproductive system, which led to all these cases of mutual sterility, was anterior or posterior to changes in other parts of the organisms. For, if it was anterior, these other changes—even though they be adaptive changes—were presumably due to the sexual change having interposed its barrier to crossing with parent forms; while, if the sexual change were posterior to the others, the presumption would be that it was those other changes which, by their reaction on the reproductive system, induced the sexual change. I shall have to consider this alternative later on. Meanwhile, therefore, it is enough to point out that under either possibility the principles of physiological selection are present; only these principles are accredited with so much the more causal influence in the production of species in the proportion that we find reason to suppose the sexual change to have been, as a rule, the prior change. Hence, under either alternative, and on the datum that species are extreme varieties, we have presented many millions of instances of fertility within the varietal form, with sterility towards allied forms. Why, then, should we feel any difficulty in supposing that the same thing happens in a lesser degree? Nay, rather, would it not be a most extraordinary fact if it did never happen in lesser degrees? Yet, if it does ever happen in lesser degrees, we have a variation of the kind required by physiological selection, although not yet of a degree sufficient to constitute the variety a new species—seeing that species is practically a name reserved by naturalists to designate this particular kind of variation, when it has arrived at a certain observable degree of departure from the parent form.

This way of looking at the matter may perhaps be rendered more effective if we glance for a moment at the extraordinary differences in the degrees of sterility which are manifested by variations that have gone far enough to be ranked by naturalists as undoubted species. For in this way we can see how impossible it is to lay down any hard and fast distinctions between species and varieties in respect of sterility, even though it has always been the aim of naturalists to give primary importance to this point. Now this difficulty is just what we ought to find, according to my theory, as a very few words will be enough to show. For, even if allied forms were always closely contiguous forms, we should expect on this theory that great differences in the degrees of sterility should be manifested by different species. According to this theory, species are but records of a sufficient degree of sterility having arisen with parent forms to admit of the varietal form not becoming swamped by intercrossing. Now, the degree of sterility required for this purpose would not be the same in all cases, seeing that in some cases other conditions might be present to assist in the prevention of intercrossing, as we shall see later on. Moreover, in other cases the initial (or the subsequently induced) degree of sterility may have been greater than was required to effect the physiological separation that took place. Lastly, when to these considerations we add that allied species are not always necessarily contiguous species, and therefore need never have had any opportunity of intercrossing (having originated independently from the same parent form in different localities)—when we consider all these things, we should expect to find the degrees of sexual incompatibility between species highly variable. Or, in other words, we should expect to find that the extreme varieties called species should not exhibit an equal degree of incompatibility in all cases. And this is just what we do find; or, as Mr. Darwin puts it, “the sterility of various species when crossed is so different in degree, and graduates away so insensibly, and, on the other hand, the fertility of pure species is so easily affected by various circumstances, that for all practical purposes it is most difficult to say where perfect fertility ends and sterility begins.”

But not only so. Among all the varieties in nature which are extreme enough to be ranked as species, we might expect, upon the theory of physiological selection, that some should have developed sterility towards certain of their allies, while develop-

ing an even increased degree of fertility towards others. For in all cases, according to this theory, degrees of fertility between allied forms are, so to speak, matters of accident; and it is only when variations in the direction of sterility with allied forms (parental or otherwise) are sufficiently pronounced to prevent intercrossing that the forms in question rise to specific rank. Therefore, looking to the immense number of species, we might expect that in some few cases where the allied forms are not also contiguous, the variation in the reproductive system which rendered one of the forms sterile with its parent form, should not also have rendered it sterile with exotic forms, or even that it should be more fertile with them than with itself. And this we do occasionally find to be the case, as the following quotations from Darwin will show.

"Of his [Herbert] many important statements I will here give only a single one as an example, namely, that "every ovule in a pod of *Crinum capense* fertilised by *C. revolutum* produced a plant, which I never saw to occur in a case of its natural fecundation." So that here we have perfect, or even more than commonly perfect, fertility in a first cross between two distinct species"*.

Mr. Darwin then proceeds to give other and analogous cases as having been well observed in *Lobelia*, *Verbascum*, and *Passiflora*; and then adds, "In the genus *Hippeastrum*, in *Corydalis* as shown by Professor Hildebrand, in various orchids as shown by Mr. Scott and Fritz Müller, all the individuals are in this peculiar condition. So that with some species, certain abnormal individuals, and in other species all the individuals, can actually be hybridised much more readily than they can be fertilised by pollen from the same individual plant."

Now, these and all other such facts go to prove that, notwithstanding even a specific distinction, there may be a higher degree of compatibility between the sexual elements of the different forms than between the sexual elements of the same form; and this would show that in the matter of sexual compatibility more depends upon the nature of the sexual elements than depends upon the rest of the organism. In other words, we may here regard the two distinct species as (physiologically considered) extreme varieties, and thus we should have evidence of a higher degree of fertility between these two extreme varietal forms than

* 'Origin of Species,' ed. 6, p. 238; also see 'Variation,' vol. ii. pp. 143-4.

normally occurs within each parent form. When, for instance, we are told by Gärtner that the yellow and white varieties of one species of *Verbascum* are considerably more fertile with the similarly coloured varieties of distinct species than they are with the differently coloured varieties of the same species, we can only conclude that the state of the reproductive system is such that there is a higher degree of sterility—or a lesser degree of sexual affinity—within the limits of the parent form, than there is between it and another variety so far changed as to constitute a distinct species. I do not, of course, pretend that in these cases the species towards which the increased fertility is exhibited has been separated from the other by physiological selection. Indeed, to do this would be to prove too much, because if the separation had been effected by physiological selection, there ought as a result to be increased sterility, and not increased fertility between these two particular specific forms. But I adduce these facts as forcible evidence of physiological selection, because they show, in the strongest imaginable way, that the conditions of sexual affinity which are required for physiological selection are to be found even between varieties so widely separated as to constitute true species. For if these conditions of sexual affinity may be such that an organism is actually more fertile with members of a distinct species than it is with members of its own species, much more may an organism which has become infertile with its parent form continue fertile with itself. In the cases mentioned the individual sexual organs may be regarded as relatively sterile towards their parent, *i. e.* their own specific form, while relatively fertile towards another specific form. Much more then may an individual be relatively sterile towards its parent form, while relatively fertile towards its own varietal form.

The same argument may be adduced from the case of animals. There are many recorded instances of both birds and mammals which, when under confinement, have proved themselves more fertile with members of different species than with members of their own. Now, whether this state of matters be supposed to be normal or superinduced by changes in the conditions of life, in either case we have organisms which are relatively sterile towards their own parent form, or relatively fertile towards another varietal form so different as to constitute a distinct species. As in the similar case of the plants above mentioned, therefore, we may here repeat how much more probable than

this would be the case that is required by physiological relation—namely, a variety relatively sterile towards its parent form, while relatively fertile within itself.

These anomalous cases, however, have only been given to show the highly variable and capricious character of the reproductive system both in plants and animals; and hence to show that the much less remarkable kind of variation which is required by my theory is not antecedently improbable. But, as a matter of argument, I do not require these anomalous cases; for enough has been previously said to prove that the particular kind of variation required actually does occur as between individuals, between races, and between species. Nevertheless, for the sake of adducing yet one further argument of an *à priori* kind, I may notice the very general fact that different varietal characters in parents belonging to the same species persistently refuse to blend in the offspring. This, indeed, may be said to be the rule both in plants and animals*. But the varietal character with which we are concerned belongs to the reproductive system itself, independently of any other part of the organism. Therefore, if this variation follows the rule of variations in general, there must be more difficulty in its blending with the parent (or unchanged) form than there is in its blending with other similarly changed forms. But, in this particular case, failure to blend means failure to propagate—*i. e.* sterility, whether partial or absolute. The varietal form will thus be more fertile within itself than it is towards its parent stock.

ARGUMENTS À POSTERIORI.

Hitherto the evidence which I have adduced in favour of physiological selection as an agency in the evolution of species is only *prima facie*. That is to say, although we have evidence to show the occurrence of this particular kind of variation, and although we can see that whenever it does occur it must be preserved, as yet we have had no evidence to indicate to what extent this particular kind of variation has been at work in the formation of species. Thus far all I have been endeavouring to show is that we have many and weighty considerations of an *à priori* kind whereby to render the theory of physiological selection

* See, for example, 'Variation of Plants and Animals under Domestication,' vol. ii. p. 72.

antecedently probable. I will, therefore, next proceed to state such evidence as I have been able to collect, tending to show that the facts of organic nature are such as we should expect they ought to be, if it is true that physiological selection has played a considerable part in their causation. And to do this I will begin by taking the three cardinal objections to the theory of natural selection with which I set out, namely sterility, intercrossing, and inutility. For, as we shall see—and this in itself is a suggestive consideration—all the facts which here present formidable obstacles to the theory of natural selection are not only explained by the theory of physiological selection, but furnish to that theory some of the best evidence which I have been able to find.

ARGUMENT FROM STERILITY BETWEEN SPECIES.

As now repeatedly observed, the theory of natural selection is not, properly speaking, a theory of the origin of species: it is a theory of the development of adaptive structures. Only if species always differed from one another in respect of adaptive structures would natural selection be a theory of the origin of species. But, as we have already seen, species do not always, or even generally, thus differ from one another. In what, then, do they differ? They differ, first, chiefly and most generally, in respect of their reproductive systems; this, therefore, I will call the primary difference. Next, they differ in an endless variety of more or less minute details of structure, which are sometimes of an adaptive character, and sometimes not. These, therefore, I will call secondary differences. Now, these secondary differences, or differences of minute detail, are never numerous as between any two allied species; in almost all cases they admit of being represented by units. Yet, if it were possible to enumerate all the specific differences throughout both the vegetable and animal kingdoms, there would be required a row of figures expressive of many millions. Or, otherwise stated, the secondary features which serve to distinguish species from species are minute differences of structure, sometimes useful and sometimes not, which may occur in any parts of organisms, but which never occur in many parts of the same organism. Thus we perceive that, if we have regard to the whole range of species, what I call the secondary differences are in the highest imaginable degree variable or inconstant. The only distinction which is at all constant or general is the one which I call primary, or the one which belongs

exclusively to the reproductive system. Surely, therefore, what we first of all require in a theory of the origin of *species* is an explanation of this relatively constant or general distinction. But this is just what all previous theories fail to supply. Natural selection accounts for some among the many secondary distinctions; but is confessedly unable to account for the primary distinction. The same remark applies to sexual selection, use and disuse, economy of growth, correlated variability, and so forth. Even the prevention of intercrossing by geographical barriers is unable to explain the very general occurrence of some degree of sterility between two allied varieties, which have diverged sufficiently to take rank as different species. All these theories, therefore, are here in the same predicament: they profess to be theories of the origin of species, and yet none of them is able to explain the one fact which more than any other goes to constitute the distinction between species and species. The consequence is that most evolutionists fall back upon a great assumption: they say it must be the change of organization which causes the sterility; it must be the secondary distinctions which determine the primary. But the contrary proposition is surely at least as probable, namely, that it is the sterility which, by preventing intercrossing with parent forms, has determined the secondary distinctions; or, rather, that this has been the original condition to the operation of the modifying causes in all cases where free intercrossing has not been otherwise prevented. For, obviously, it is a pure assumption to say that the secondary differences between species have been historically prior to the primary difference, and that they stand to it in the relation of cause to effect. Moreover, the assumption does not stand the test of examination, as I will now proceed to show.

First, on merely *à priori* grounds, it scarcely seems probable that whenever any * part of any organism is slightly changed in any way by natural selection or any other cause, the reproductive system should forthwith respond to that change by becoming sterile with allied forms. What we find in nature is a more or less constant association between the one primary distinction and an endless profusion of secondary distinctions. Now, if this association had been between the primary distinction and some one, or even some few, secondary distinctions, constantly the

* This appears to be what the theory requires, seeing that *all* parts of organisms are subject to secondary specific distinctions.

same in kind, in this case I could have seen that the question would have been an open one as to which was cause and which effect, or which was the conditional and which the conditioned. But, as the case actually stands, on merely antecedent grounds it does not appear to me that the question is an open one. Here we have a constant peculiarity or condition of the reproductive system, repeated over and over again millions of times, throughout organic nature past and present; and we perpetually find that when this peculiar condition of the reproductive system occurs it is associated with structural changes elsewhere, which, however, may affect any part of any organism, and this in any degree. Now, I ask, is it a reasonable view to imagine that the one constant peculiarity is always the result and never the condition of any among these millions of inconstant and organically minute changes with which it is found associated? Even if I had no theory whereby to account for the primary and constant distinction being also the primordial and conditioning distinction, on merely *à priori* grounds I should feel convinced that in some way or another it *must* be so.

But, secondly, quitting *à priori* grounds, it is a matter of notorious fact that in the case of nearly all our innumerable artificial productions, organisms admit of being profoundly changed in a great variety of ways, without any reaction on the reproductive system following as a consequence. So seldom, indeed, does any such reaction follow from what may be termed all these innumerable experiments upon the subject, that Mr. Darwin was obliged to explain the discrepancy between the known influence of artificial selection and the supposed influence of natural selection by invoking a wholly independent, an extremely hypothetical, and, to my mind, a most unsatisfactory principle. This principle—*i. e.* that of prolonged exposure to similar conditions of life—I have already considered, and shown why it appears to me the feeblest suggestion that is to be met with in the whole range of Mr. Darwin's writings.

Thirdly, as regards wild species, Mr. Darwin shows that "the correspondence between systematic affinity and the facility of crossing is by no means strict. A multitude of cases could be given of very closely allied species which will not unite, or only with extreme difficulty; and, on the other hand, of very distinct species which unite with the utmost facility." And he goes on to show that "within the limits of the same family, or even of

the same genus, these opposite cases may occur"* . Now, on the supposition that sterility between species is always or generally caused by the indirect influence on the reproductive system of changes taking place in other parts of the organism, these facts are unintelligible—being, indeed, as a mere matter of logic, contradictory of the supposition.

Fourthly, it is surely a most significant fact that, as Mr. Darwin observes, "independently of the question of fertility, in all other respects there is the closest general resemblance between hybrids and mongrels" †. For this fact implies that natural selection and artificial selection run perfectly parallel in all other respects, save in the one respect of reacting on the reproductive system, where, according to the views against which I am arguing, they must be regarded as differing, not only constantly, but also profoundly.

Fifthly, and lastly, Darwin further observes that "the primary cause of the sterility of crossed species (as compared with crossed varieties) is confined to differences in their sexual elements" ‡. Now this assuredly proves that the primary specific distinction is one with which the organism as a whole is not concerned; this primary distinction is, so to speak, a local variation in the organism, which has to do only with the reproductive system, and which therefore need not necessarily be in all, or even in most, cases an incidental result of minute variations going on elsewhere.

In view of these several considerations, it appears to me perfectly plain that the smaller organic changes which alone are concerned in specific distinctions are not always, or even generally, adequate to react on the reproductive system

* He also adds:—"No one has been able to point out what kind or amount of difference in any recognizable character is sufficient to prevent two species crossing. It can be shown that plants most widely different in habit and general appearance, and having strongly marked differences in every part of the flower, even in the pollen, in the fruit, and in the cotyledons, can be crossed. Annual and perennial plants, deciduous and evergreen trees, plants inhabiting different stations and fitted for extremely different climates, can often be crossed with ease." And, after considering the further case of reciprocal crosses, he expresses the general conclusion: "Such cases are highly important, for they prove that the capacity in any two species to cross is often completely independent of their systematic affinity, that is of any difference in their structure or constitution, excepting in their reproductive systems." ('Origin of Species,' ed. 6, p. 243.)

† 'Origin of Species,' where the general fact is proved beyond question.

‡ *Loc. cit.* This fact, also, is proved beyond the possibility of question.

in the way hitherto supposed by evolutionists*; but that the primary distinction is in most cases, as I have just expressed it, a local variation in the organism, which has to do only with the reproductive system. Why, then, should we suppose that it differs from a local variation taking place in any other part of the organism? Why should we suppose that, unlike all other such variations, it cannot be independent, but must be superinduced as a secondary result of variations taking place elsewhere? It appears to me that the chief reason why evolutionists suppose this, is because the particular variation in question happens to have as its result the origination of species; and that, being already committed to a belief in other agencies as the cause of such origination, in consistency they are obliged to regard this particular kind of local variation as not independent, but superinduced as a secondary result of these other agencies operating on other parts of the organism. In short, it appears to me that by persistently regarding the primary specific distinction as a derivative and incidental result of the secondary, evolutionists are putting the cart before the horse; and the only reason they can show for choosing this arrangement is that they already assume the origin of species to have been due to other causes, and in particular to natural selection. But once let them clearly perceive that natural selection is concerned with the origin of species only in so far as it is concerned with the origin of adaptive structures, or only in so far as it is concerned with some among the many secondary distinctions—once let naturalists be perfectly clear upon this point, and they will perceive that the primary specific distinction takes its place beside all other variations as a variation of a local character, which may, indeed, at times be due to the indirect influence of natural selection, use, disuse, and so forth; but which may also be due to any of the other numberless and hidden causes that are concerned with variation in general.

Thus, I repeat, what we require in a theory of the origin of species is a theory to explain the primary and most constant distinction between species, or the distinction in virtue of which they exist as species. This distinction, as we have now so repeatedly seen, is one that belongs exclusively to the reproductive system; and it always consists in comparative sterility towards

* I do not think that Mr. Darwin himself entertained this supposition, and therefore I have not his authority against me.

allied forms, with continued fertility within the varietal form. Now, this state of matters as between allied species is merely an intensification, or a further development, of that which physiological selection supposes to obtain between the physiological varieties, where the variation is from the first in the direction just mentioned. That this initial variation should afterwards become intensified by the practical separation of the two varieties, so that what began as a varietal difference ends as a specific difference, is no more than we should expect. For from the first the variation was one specially affecting the reproductive system in the special way required; intercrossing with the parent form was from the first precluded in a degree proportional to the amount of the variation. The species was thus from the first divided into two physiological parts, each of which then entered upon an independent course of genetic history; the principle of continued variation along the same lines would tend to increase the original separation; the new variety, therefore, besides having been thus started with a tendency, and a probable increasing tendency, to a physiological separation from its parent stock, must afterwards have become exposed to all or any such modifying causes as are found to produce a similar separation in a portion of a species when started on an independent course of history by migration or by geographical isolation.

Lastly, over and above all these considerations, there remains one of much importance, not only to the present division of my argument, but to my theory as a whole. For Mr. Darwin has furnished exceedingly good reasons for entertaining his own view that this is "one of the causes of ordinary variability; namely, that the reproductive system, from being eminently sensitive to changed conditions of life, fails under these circumstances to perform its proper function of producing offspring closely similar in all respects to the parent form"*. Now, if this view is well founded—and, as I have said, Mr. Darwin's arguments in favour of it are most cogent—it obviously has most important bearings on the present theory; for it implies that whenever the reproductive system undergoes a variation on its own account, whether this be due to extrinsic or intrinsic causes, it is apt to induce variations in other parts of progeny. Hence, prevention of intercrossing by the physiological barrier of reproductive or primary variation is so far more likely to be followed

* 'Origin of Species,' ed. 6, p. 260.

by secondary variations than when the prevention of intercrossing arises from geographical barriers or from migration. For in this case, over and above the influence of independent variability, there is a direct causal connection between the agency which prevents intercrossing and the subsequent production of secondary specific characters. So that, if Mr. Darwin's view of one of the causes of variability be accepted, it follows that wherever the primary specific distinction of sterility arises, there it is to be expected that an unusual crop of variations should follow by way of consequence in other parts of the physiologically separated progeny—variations, therefore, which, whether they happen to be useful or unuseful, appear under circumstances most favourable to their perpetuation as secondary specific characters.

I trust, then, that sufficient reasons have now been given to justify my view that, if we take a broad survey of all the facts bearing on the question, it becomes almost impossible to doubt that the primary specific distinction is, as a general rule, the primordial distinction. I say "as a general rule," because the next point which I wish to present is that it constitutes no part of my argument to deny that in some, and possibly in many, cases the primary distinction may have been superinduced by the secondary distinctions. Indeed, looking to the occasional appearance of partial sterility between domesticated productions, as well as to the universally high degree of it between genera, and its universally absolute degree between families, orders, and classes, I see the best of reasons to conclude that in some cases the sterility between species may have been originally caused, *and in a much greater number of cases subsequently intensified*, by changes going on in other parts of the organism. Moreover, I doubt not that of the agencies determining such changes, natural selection is probably one of the most important. In other words, I do not doubt that natural selection, by operating independently on a separated portion of a species—whether the separation be physiological or geographical—may often help to induce sterility with the parent form, by indirectly modifying the reproductive system through changes which it effects in other parts of the organism; and I see no reason to doubt that the same is true of sexual selection, use and disuse, economy of growth, correlated variability, or any other cause tending to modify the organism in any of its parts, and so, in *some* instances, reacting indirectly on the reproductive system in the way required. Here I only

differ from other evolutionists in refusing to suppose that this must invariably, or even generally, be the result of what I may term adaptational causes, when these are producing small (*i. e.* specific) morphological changes in any part of any organism. Yet, as I have said, I doubt not that such has been the incidental or indirect result of these causes in some minority of cases. But, now, what does this amount to? It amounts to nothing more than a re-statement of the theory of physiological selection. It merely suggests hypothetically the cause, or causes, of that particular variation in the reproductive system with which alone the theory of physiological selection is concerned, and which, as a matter of fact, *however caused*, is found to constitute the one cardinal distinction between species and species. Therefore I am really not concerned with what I deem the impossible task of showing how far, or how often, natural selection, or any other cause, may have induced this particular kind of variation in the reproductive system by its operations on other parts of an organism. Even if I were to go the full length that other evolutionists have gone, and regard this primary specific distinction as in all cases due to the secondary specific distinctions, still I should not be vacating my theory of physiological selection; I should merely be limiting the possibilities of variation within the reproductive system in what I now consider a wholly unjustifiable manner. For, as previously stated, it appears to me much the more rational view that the primary specific distinction is likewise, as a rule, the primordial distinction, and that the cases where it has been superinduced by the secondary distinctions are comparatively few in number.

Next, let it be observed that, even in these last-mentioned cases—whether, as I believe, they are comparatively few or comparatively numerous—where the primary distinction has been superinduced by the secondary, even in these cases my theory is available to show why the two kinds of distinction are so generally associated, or why it is that the primary distinction is so habitual an accompaniment of the secondary distinctions, of whatever kinds or degrees the latter may happen to be. For, according to my theory, the reason of the association in these cases is that it can only be those kinds and degrees of secondary distinction which are able so to react on the reproductive system as to induce the primary distinction that are *for this reason* preserved, or allowed to become developed as a new specific type. Whether as causes or as effects, therefore, the secondary distinctions are *dependent*

on the primary one, in the sense that, even if they be the causes, they depend for their existence on the fact that they happen to have been capable of producing this particular effect—a general view of the case which appears to me abundantly justified by the fact of their general *association*. Hence, if there are any cases—and I do not doubt that there are many—where the secondary distinctions have been the cause of the primary distinction, still even here the former are, as I have phrased it, dependent on the latter, inasmuch as the latter is a necessary condition to their existence. Or, otherwise expressed, unless the secondary distinctions had happened to be of a kind which induced the primary distinction, they could not in themselves have survived, but would have been reabsorbed by free intercrossing. Thus, according to my view, even in the minority of cases where the causes of the primary distinction have been such changes in the organism as I have called secondary distinctions, even in this minority of cases the principles of physiological selection have been at work. For these principles have in all those cases *selected* the particular kinds of secondary distinctions which have proved themselves capable of so reacting on the reproductive system as to bring about the primary distinction.

Suppose, for instance, that all our horticulturists and breeders were suddenly to allow all domesticated varieties freely to intercross, and suppose that some of these varieties had been previously acted upon by artificial selection to an extent of inducing sterility in a degree comparable with what evolutionists imagine that natural selection may have been able to accomplish in incipient species. Under these circumstances, physiological selection would at once set to work to pick out all these sexually protected forms, and hand them on as permanent varieties (or, if the sterility were sufficiently pronounced, as true species); while all the other forms, no matter how much they might differ from one another in respect of secondary distinctions, would be doomed to extinction—or, as we should then say, to reversion, which merely means reabsorption of secondary distinctions into parent forms. Now, if so soon as the artificial barriers to intercrossing were removed this is what would inevitably take place even with secondary distinctions already formed, is it not evident that, in the original absence of any kind of barrier otherwise given, none of these secondary distinctions could ever have arisen, except those

which happened so to react on the reproductive system as themselves incidentally to erect a barrier, which might then serve—as in the parallel case given in my illustration—to protect that particular assemblage of secondary distinctions from extermination when they first arose, and afterwards to admit of their being handed on in ever-increasing degrees of development? And, in point of fact, that this has been the case (supposing for illustration's sake the primary to have *always* been the result of secondary distinctions) is proved by the very general association that is now found to subsist between them—an association which can only be accounted for by supposing that all other kinds of secondary distinction failed in what may be termed their struggle for existence, simply because they were not able to rear for themselves this barrier of sterility.

Thus, we see, it really makes no essential difference to my theory whether it be supposed, in any given case, that the primary distinction was prior or subsequent to the secondary distinctions. I have given my reasons for believing that in the great majority of cases the primary distinction was, as I have said, the primordial distinction; and, if so, the causal influence of physiological selection in the formation of species was in these cases absolute. But I have also given my reasons for believing that in a minority of cases the secondary distinctions determined the primary distinction; and, if so, the causal influence of physiological selection was in these cases relative, or conditional on other causes extrinsic to the organism. But whether the ultimate causes of the primary distinction be extrinsic or intrinsic, and whether this primary distinction be historically prior or subsequent to the secondary distinctions, in all cases (save where intercrossing is otherwise prevented) it must be physiological selection that has been the agency to which the preservation of the secondary distinctions has been due. For, as we have now so repeatedly seen, any secondary distinctions, howsoever useful in themselves, must be always liable to extinction almost at the moment of their birth, unless they happen to be protected by the primary distinction. Hence, whether the latter be given by independent variation on the part of the reproductive system itself, or as an indirect and concomitant result of variations taking place elsewhere, it is equally true that the principles of physiological selection have been at work; and, therefore, that it is to those

principles we must look for our ultimate explanation of the origin of species*.

If we thus regard sterility between species as the result of what I have called a local variation arising only in the reproductive system, whether induced by changes taking place in other parts of the organism, to changes in the conditions of life, or to changes inherent in the reproductive system itself, we can understand (a) why such sterility rarely, though sometimes, occurs in our domesticated productions; (b) why it so generally occurs in some degree between species; and (c) why as between species it occurs in all degrees.

(a) It rarely occurs in our domesticated productions, because it has never been the object of breeders or horticulturists to preserve this kind of variation. Yet it sometimes does occur in some degree among our domesticated productions, because the changes produced on other parts of the organism by artificial selection do, in a small percentage of cases, react upon the reproductive system in the way of tending to produce sterility with the parent form, without lessening fertility with the varietal form. Again (b), this particular condition of the reproductive system is so generally characteristic of species, simply because, as a general rule, it is owing to this condition that species exist as species; any variation, therefore, towards this condition, howsoever produced, must always have been preserved by physiological selection, with the result of a new specific form to record the fact. And, lastly (c), this particular variation in the reproductive system has taken place under nature in such a number of degrees, from absolute sterility between species up to complete, or even to more than complete fertility, because natural species, while being records of this particular *kind* of variation, are likewise the records of all *degrees* of such variation which have proved sufficient to prevent overwhelming intercrossing with parent forms. Sometimes this degree has been less than others, because other conditions—climatic, geographical, habitational, physiological, and even psychological—have co-operated to prevent intercrossing, or even to

* In order to avoid needlessly confusing the foregoing argument, I have omitted to notice that geographical barriers serve the same function as physiological barriers; and also that secondary distinctions caused by use and disuse do not require to be protected from the levelling effects of intercrossing. But, as will be seen from the next succeeding paragraphs, these considerations are in no way opposed to my theory.

render the prevention of intercrossing wholly unnecessary, and thus not in any way to require the protecting influence of physiological selection. I will consider these points separately.

First, other conditions may co-operate with physiological selection to prevent intercrossing with parent forms, and therefore, in whatever degree such co-operation is furnished, a correspondingly less degree of sterility will be required in order to secure a differentiation of specific type. Of these other conditions migrations and geographical barriers are probably the most important; and as such barriers may occur in all degrees of efficiency, from wholly secluding small sections of species in oceanic islands to imposing but slight difficulties in crossing streams &c., it is evident that in many cases physiological selection may be thus assisted in a great variety of degrees. Again, even where there are no geographical barriers of any kind, varieties will occasionally be segregated by their different degrees of adaptation to differences of climate—the adaptation having no special reference to the reproductive system, and yet, by determining that the variety shall live under a different climate from the parent form, more or less effectually preventing intercrossing with that form. The same thing applies to varieties occupying stations of their own*, and also, in the case of higher Vertebrata, to all the members of the same variety preferring to pair together, rather than with their parent form, or with other varieties†. In all these cases where the principles of physiological selection have been in any degree accidentally assisted by other conditions, a correspondingly less degree of variation in the reproductive system would have been needed to differentiate the species. That is to say, if the variation has been sufficient in amount, or in relation to all the other conditions of the time, to prevent intercrossing with the parent form in any extinguishing degree, the resulting sterility need not always be absolute, even as between compatriots, but may occur in any corresponding degree; while, as between species which have been independently evolved on different geographical areas, fertility may remain unimpaired, or even be accidentally increased.

Secondly, in other cases species may have become differentiated without the variations requiring to be protected from intercrossing, either by physiological, geographical, or any other barriers. In these cases, therefore, physiological selection has had no part in

* See 'Origin of Species,' ed. 6, p. 8.

† *Ibid.*

the evolution of species. The cases to which I allude are those where specific types have been modified by the agencies of what Mr. Spencer calls "direct equilibration." Of these agencies the most important that happen to be known to us are use and disuse. A little thought will show that the moulding power of these agencies on specific types must be quite as independent of physiological selection as it is of natural selection. But a little more thought will show that this moulding influence must always be in some one line of morphological change: it cannot proceed in many diverging ways at once; but must slowly transmute a whole specific type into some other specific type. Now, if this change should happen to go on in a portion of a species living in one part of the world, when that portion becomes transmuted into a different specific type, there is no reason why the now modified descendants should prove barren when crossed with their unchanged, or differently changed, parent-form, which may be still living in any other part of the world.

In view of all these considerations, I should regard it as a serious objection to my theory if it could be shown that sterility between allied species is invariably absolute, or even if it could be shown that there are no cases of fertility unimpaired. What my theory would expect to find is exactly what we do find, namely, a considerable majority of instances where sterility occurs in all degrees, with comparatively exceptional instances where secondary distinctions have been able to develop without being associated with the primary distinction.

On the whole, therefore, I cannot but candidly consider that all the facts relating to the sterility of natural species are just what they ought to be, if they have been in chief part due to the principle which I am advocating. Mr. Darwin appears to have clearly perceived that there must be some one principle serving to explain all these facts, so curiously related and yet so curiously diverse; for he says, and he says most truly, "We have conclusive evidence that the sterility of species must be due to some principle quite independent of natural selection." And I trust enough has now been said to show that, in all probability, this hitherto unnoticed principle is the principle of physiological selection.

ARGUMENT FROM THE PREVENTION OF INTERCROSSING.

This argument is the same from whatever cause the prevention of intercrossing may arise. Where intercrossing is prevented by

geographical barriers or by migration, it is more easy to prove the evolution of new species as a consequence than it is when intercrossing has been prevented by physiological barriers; for in the latter case the older and the newer forms will probably continue to occupy the same area, and thus there will be no independent evidence to show that the severance between them was due to the prevention of intercrossing. Nevertheless, all the evidence which I have of the large part that geographical barriers and migration have played in the evolution of species by the prevention of intercrossing with parent forms, goes to show the probable importance of physiological barriers when acting in the same way. Hence it will be better to postpone this line of argument till the appearance of my next paper, where I shall hope to show, from evidence furnished by the geographical distribution of species, how predominant a part the prevention of intercrossing has played in the evolution of species. Here, therefore, it will be enough to offer a few general remarks.

In the first place, the theory of physiological selection has this great advantage over the theory of natural selection, namely, that the swamping effects of free intercrossing on the new variety—or on the incipient species—are supposed to be from the first excluded by the very fact of the variation itself. This is so obvious an advantage that it appears needless to dwell upon its consideration.

But, in the next place, I may observe that, in so many cases as species do originate by physiological selection, the subsequent influence of natural selection admits of being considerably enhanced. For when once this physiological separation between a variety and its parent-stock has been effected, there will be less likelihood than before of any useful variations which may subsequently arise in the former being again obliterated by intercrossing. This is evident, because the possibilities of intercrossing would now be restricted to a much smaller number of individuals, and therefore the influence of intercrossing would not be so detrimental to the continuance of any beneficial variation. In other words, the primary variation of the reproductive system would serve to protect any secondary variations of a useful kind which might afterwards arise elsewhere; just as happens in the analogous case where intercrossing is prevented by geographical barriers, or by migration in different directions of varying descendants from a common centre.

And here we catch sight of another respect in which physiological selection probably cooperates with natural selection. As previously remarked, Mr. Darwin felt profoundly the strength of this objection from sterility between species, and, I may now add, he tried to imagine some way in which the general fact of such sterility might be reasonably attributed to natural selection. If he could have done this, of course he would have mitigated the difficulty; for, as he writes, "it would clearly be advantageous to two varieties or incipient species if they could be kept from blending, on the same principle that, when man is selecting at the same time two varieties, it is necessary that he should keep them separate." But, as the result of his discussion, he concludes:—"In considering the probability of natural selection having come into action in rendering species mutually sterile, the greatest difficulty will be found to be in the existence of many graduated steps from slightly lessened fertility to absolute sterility. It may be admitted that it would profit an incipient species, even if it were rendered in some slight degree sterile when crossed with its parent-form or with some other variety; for thus fewer bastardized and deteriorated offspring would be produced to commingle their blood with the new species in process of formation. But he who will take the trouble to reflect on the steps by which this first degree of sterility could be increased through natural selection to that high degree which is common with so many species, will find the subject extraordinarily complex. After mature reflection it appears to me that this could not have been effected through natural selection."

Now, with this conclusion I fully agree; but it will by this time be clearly seen that what cannot be effected by natural selection may well be effected by physiological selection. For both the considerations which Mr. Darwin here candidly adduces as insuperable difficulties in the way of supposing sterility due to natural selection, are just the considerations which most strongly favour the hypothesis of physiological selection. These two considerations are, first, "the many graduated steps from slightly lessened fertility to absolute sterility," and, second, "the steps by which this first degree of sterility would be increased." Now, as already shown in a previous part of this paper, these "many graduated steps" are just what we might expect to find on the theory of physiological selection; while, upon this theory, there is no need to suppose that "the first degree of sterility" must necessarily go on increasing. In

whatever degree the sterility first occurs, in that degree it may remain; for, *ex hypothesi*, it must from the first have been sufficient to cause at least so much of physiological separation of the varietal type as to admit of the continuance of that type. If this degree of sterility were from the first but small, a longer time would be required to effect a complete separation between the parent and the variety, than if this degree were from the first considerable. But, as we have before seen, this is all the difference that would arise; and therefore, upon my theory, we may regard degrees of sterility as matters of no significance—although I do think it is extremely probable that when once sterility in any degree has arisen it will afterwards become increased, not so much for the reason assigned by Mr. Darwin (*viz.* prolonged exposure to uniform conditions), as from the general tendency which variations of all kinds present to continue in the lines of their initial deviation. I cannot doubt that if the theory of physiological selection had occurred to Mr. Darwin, he would have seen in this latter consideration a much more cogent reason than the one which he assigns for the general sterility that obtains between species. But he was precluded from applying this consideration because it did not occur to him that sterility might itself be originally due to independent variation, and thus itself be subject to the laws of variation in general.

I trust, then, that these considerations will have shown that, although natural selection cannot have been directly instrumental in causing sterility between an incipient species and its parent form, if the incipient species were such in virtue of a variation in its reproductive system tending from the first to prevent intercrossing with its parent form, then there would be a variation the further development of which might be favoured by natural selection. For if, as Mr. Darwin thought, “it would profit an incipient species if it were rendered in some degree sterile with its parent form,” although this profit could not have been initially conferred by natural selection, yet when it once arises from a spontaneous variation in the reproductive system itself, I see no reason to doubt that it should forthwith be favoured by natural selection, just as is the case with favourable variations in general. That is to say, natural selection would set a premium upon infertility with the parent form, and would thus cooperate with physiological selection in splitting up the specific type. For, although natural selection is powerless to induce sterility between allied forms,

when once this sterility is given as an independent variation, the forms—though not necessarily the *individuals*—which profit by it would be favoured by natural selection in their competition with other forms which do not present such variation. In short, once let intercrossing with the parent-type be prevented by physiological selection, and the field is at once thrown open to the further or cooperating influence of natural selection—whether this be effected directly, as here supposed, or indirectly by modifying the reproductive system through the rest of the organism, as previously supposed. Later on, under Divergence of Character, I will show another and much more important respect in which physiological selection, by preventing intercrossing with parent forms, is able to assist natural selection in the differentiation of specific types.

ARGUMENT FROM THE INUTILITY OF SPECIFIC DIFFERENCES.

With reference to inutility, after what has already been said, I will only repeat this somewhat important question,—Why is it that apparently useless structures and instincts occur in such profusion among species, in much less profusion among genera, and scarcely at all among families, orders, and classes? To this question the Darwinist can only answer that the utility of apparently useless structures really is less than that of structures whose utility is observable. For although the argument from ignorance may be available up to a certain point, it clearly cannot be available to the extent of showing why useful structures within the limits of species should have their utility more disguised than useful structures elsewhere. Hence the Darwinist can only conclude that, at all events the majority of structures which he assumes to be useful in the case of species are not *seen* by him to be useful, because their utility actually *is* less than in the case of structures distinctive of genera, families, and so forth. He must argue that the points wherein species differ from species—being points of smaller detail than those which serve to distinguish genera, families, &c.—present less opportunity of usefulness; and, therefore, as a rule, actually are of too little use to admit of their utility being diagnosed, although not of so little use as to have prevented their development by natural selection, which is a better diagnostician of utility than the naturalist. But how much more probable is the answer which

may be furnished by any one who accepts the theory of physiological selection. For, upon this theory, it is quite intelligible that when a varietal form is differentiated from its parent form by the bar of sterility, any little meaningless peculiarities of structure or of instinct should at first be allowed to arise, and that they should then be allowed to perpetuate themselves by heredity, until—not being conserved by natural selection—they should be again eliminated as so much surplusage in the struggle for existence, whether by the economy of growth or by independent variation when undirected by natural selection. A greater or less time would in different cases be required to effect this reduction; and thus we can understand how it is that any useless structures which do not impose much tax upon the organism occasionally persist even into genera, but rarely into families, or higher taxonomic divisions.

This appears to me much the most probable view, not merely on *à priori* grounds, but also for the following reasons. I have just said that if apparently useless structures (whether these be new structures or modifications of old ones, slight changes of form, colour, and so forth) are thus to be regarded as really useless, or as meaningless variations not yet eliminated by natural selection or other agencies,—I have said that, if this is so, these apparently useless structures must be of a kind which do not impose much tax upon the organism. Now I have applied this test, and I find it is almost an invariable rule (both in plants and animals) that apparently useless structures are structures of this kind. Either on account of their small size or of their organically inexpensive material, they are structures which do not impose any such physiological tax upon the organism as should lead us to expect their speedy removal. But surely there can be no imaginable association between utility as disguised and smallness of size, or inexpensiveness of material. Whereas, no less surely, there is a most obvious connection between these things and a *real* inutility. Thus, it is only a blind prepossession in favour of survival of the fittest as in all cases the originating cause of species that can lead to so irrational an assumption as that of universal utility.

Again, even apart from all the above considerations, the truth of this remark may be well exemplified within the limits of Mr. Darwin's own writings; for Mr. Darwin is here, as usual, his own best critic. He says, "In the earlier editions of this work I

underrated, as it now seems probable, the frequency and importance of modifications due to spontaneous variability”*, by which he means unuseful modifications. And he proceeds to give a number of examples.

Elsewhere (p. 158) he points out that modifications which appear to present obvious utility are found on further examination to be really useless. This latter consideration, therefore, may be said to act as a foil to the one against which I am arguing, viz. that modifications which appear to be useless may nevertheless be useful. But here is a still more suggestive consideration, also derived from Mr. Darwin’s writings. Among our domesticated productions, changes of structure—or even structures wholly new—not unfrequently arise which are in every way analogous to the apparently useless distinctions between wild species. Take, for example, the following most instructive case:—

“Another curious anomaly is offered by the appendages described by M. Eudes-Deslongchamps as often characterizing the Normandy pigs. These appendages are always attached to the same spot, to the corners of the jaws; they are cylindrical, about three inches in length, covered with bristles, and with a pencil of bristles rising out of a sinus on one side; they have a cartilaginous centre with two small longitudinal muscles; they occur either symmetrically on both sides of the face, or on one side alone. Richardson figures them on the gaunt old ‘Irish Greyhound pig;’ and Nathusius states that they often occasionally appear in all the long-eared races, but are not strictly inherited, for they occur or fail in the animals of the same litter. As no wild pigs are known to have analogous appendages, we have at present no reason to suppose that their appearance is due to reversion; and if this be so, we are forced to admit that a somewhat complex, though apparently useless, structure may be suddenly developed without the aid of selection”†.

Now, if any such structure as this occurred in a wild species, and if any one were to ask what is the use of it, those who rely on the argument from ignorance would have a much stronger case than they usually have; for they might point to the cartilage supplied with muscles, and supporting a curious arrange-

* ‘Origin of Species,’ ed. 6, p. 171. Also, and even more strongly, ‘Descent of Man,’ p. 367.

† ‘Variation,’ &c. vol. i. pp. 78-9.

ment of bristles as much too specialized a structure to be wholly meaningless. Yet we happen to know that this particular structure is wholly meaningless. What, then, are we to say to the argument from ignorance in other and less cogent cases? I think we must say that the argument is wholly untrustworthy in fact, while even in theory it can only stand upon the assumption (latterly discarded even by Darwin himself) that all specific differences must be due to natural selection.

ARGUMENT FROM DIVERGENCE OF CHARACTER.

Any theory of the origin of species in the way of descent must be prepared with an answer to the question, Why have species *multiplied*? How is it that, in the course of evolution, species have not simply become transmuted in linear series instead of ramifying into branches? This question Mr. Darwin seeks to answer "from the simple circumstance that the more diversified the descendants from any one species become in structure, constitution, and habits, by so much will they be better enabled to seize on many and widely diversified places in the economy of nature, and so be enabled to increase in numbers."* And he proceeds to illustrate this principle by means of a diagram, showing the hypothetical divergence of character undergone by the descendants of seven species. Thus, he attributes divergence of character exclusively to the influence of natural selection.

Now, this argument appears to me unassailable in all save one particular; but this is a most important particular: the argument wholly ignores the fact of intercrossing with parent forms. Granting to the argument that intercrossing with parent forms is prohibited, and nothing can be more satisfactory. The argument, however, sets out with showing that it is in limited areas, or in areas already overstocked with the specific form in question, that the advantages to be derived from diversification will be most pronounced. Or, in Mr. Darwin's words, it is where they "jostle each other most closely" that natural selection will set a premium upon any members of the species which may depart from the common type. Now, inasmuch as this jostling or overcrowding of individuals is a needful condition to the agency of natural selection in the way of diversifying character, must we not feel that the general difficulty from intercrossing previously

* 'Origin of Species,' ed. 6, p. 87.

considered is here presented in a special and aggravated form? At all events, I know that, after having duly and impartially considered the matter, to me it does appear that unless the swamping effects of intercrossing with the parent form on an overcrowded area is in some way prevented, to begin with, natural selection could never have any material supplied by which to go on with. Let it be observed that I regard Mr. Darwin's argument as perfectly sound where it treats of the divergence of *species*, and of their further divergence into *genera*; for in these cases the physiological barrier is known to be already present. But in applying the argument to explain the divergence of *individuals* into *varieties*, it seems to me that here, more than anywhere else, Mr. Darwin has strangely lost sight of the formidable difficulty in question; for in this particular case so formidable does the difficulty seem to me, that I cannot believe that natural selection alone could produce any divergence of specific character, so long as all the individuals on an overcrowded area occupy that area together. Yet, if any of them quit that area, and so escape from the unifying influence of free intercrossing*, these individuals also escape from the conditions which Mr. Darwin names as those that are needed by natural selection in order to produce divergence. Therefore, it appears to me that, under the circumstances supposed, natural selection alone could not produce divergence; the most it could do would be to change the whole specific type in some one direction (the needful variations in that one direction being caused by some general change of food, climate, habit, &c., affecting a number of individuals simultaneously), and thus induce transmutation of species in a linear series, each succeeding member of which might supplant its parent form. But in order to secure diversity, multiplication, or ramification of species, it appears to me obvious that the primary condition required is that of preventing intercrossing with parent forms at the origin of each branch, whether the prevention be from the first absolute, or only partial. And, after all that has been previously said, it is needless again to show that the principles of physiological selection are at once the only principles which are here likely to be efficient, and the principles which are fully capable of doing all that is required. For species, as they now

* As Mr. Darwin elsewhere observes, "Intercrossing plays a very important part in nature by keeping the individuals of the same species, or of the same variety, true and uniform in character" (p. 81).

stand, unquestionably prove the fact of ramification; and it appears to me no less unquestionable that ramification, as often as it has occurred, can only have been permitted to occur by the absence of intercrossing with parent forms. But, apart from geographical barriers (which, according to Mr. Darwin's argument, would be inimical to the divergence of character by natural selection), the ramification can only take place as a consequence of physiological selection, or as a consequence of some change in the reproductive system which prevents intercrossing with unchanged (or differently changed) compatriots. But when once this condition is supplied by physiological selection, I have no doubt that divergence of character may then be promoted by natural selection, in the way that is explained by Mr. Darwin.

And this latter consideration is a most important one for us to bear in mind, because it furnishes an additional reason for the fact that when a section of a species has become physiologically separated from the rest of its species, it forthwith begins to run into variations of other kinds, and so eventually to differ from the parent type, not only as regards the primary distinction of sterility, but also as regards secondary distinctions which may affect any part of the organism. The only reasons which I have hitherto assigned for this fact are, first, that from the time when overwhelming intercrossing with the parent form is prevented, the varietal form is allowed to develop an independent course of varietal history, as in the parallel case where intercrossing is prevented by geographical barriers, or by migration; and, second, that when the primary variation takes place in the reproductive system, it is apt to cause secondary variations in the progeny. But now I may make this important addition to those reasons—the addition, I mean, that when intercrossing with a parent form is in any degree prevented by physiological selection, the varietal form is free to develop diversity of character under the influence of natural selection, in the way that has been so ably shown by Mr. Darwin.

From which it will be seen that the theory of physiological selection has this advantage over the theory of natural selection in the way of explaining what Mr. Darwin calls diversification of character, or what I have called the ramification of species. This diversification or ramification has reference chiefly to the secondary specific distinctions which, as we have seen, the theory of natural selection supposes to be the first changes that occur, and

by their occurrence to induce the primary distinction of sterility. My theory, on the other hand, inverts this order, and supposes the primary distinction to be likewise, as a rule, the primordial distinction. Now, the advantages thus gained are two-fold. In the first place, as just shown, we are able to release the principles of natural selection from what appears to me the otherwise hopeless difficulty of effecting diversification of specific character on an overcrowded area, with nothing to prevent free intercrossing; and, in the next place, as we can now see, we are able to find an additional reason for the diversification of character, over and above the one that is relied upon by Mr. Darwin. For, by regarding the primary distinction of sterility as likewise the primordial distinction, we are able to apply to an incipient variety, inhabiting even an overcrowded area, the same principles which are known to lead to diversification on oceanic islands, &c., as previously explained. Moreover, from any initial variation on the part of the reproductive system, we should be prepared to expect variations to occur in other parts of the progeny. Thus, if once we regard the primary distinction of sterility as also the initial distinction, instead of an incidental result of secondary distinctions, Mr. Darwin's argument touching the causes of diversification is not merely saved: it is notably extended by the addition of two independent principles which, as we know from other evidence, are principles of high importance in this respect.

ARGUMENT FROM GEOGRAPHICAL DISTRIBUTION.

From the nature of the case, there is only one other line of evidence open whereby to substantiate the theory of physiological selection, namely, the evidence which is afforded by the geographical distribution of species. But the evidence here is both abundant in quantity and, to my mind, most cogent in quality. On the present occasion, however, I can only give a brief sketch of its main outlines.

Mr. Darwin has adduced very good evidence to show that large areas, notwithstanding the disadvantages which (on his theory) must arise from free intercrossing, are what he terms better manufactories of species than smaller areas, such as oceanic islands. On the other hand, I have previously noticed that oceanic islands are comparatively rich in peculiar species. But these two statements are not incompatible. Smaller areas are, as a rule, rich in peculiar species relatively to the number of

their inhabitants ; but it does not follow that they are rich in species if contrasted with larger areas containing very many more inhabitants. Therefore, the rules are that large areas turn out an absolutely greater number of specific types than small areas ; although, relatively to the number of individuals or amount of population, the small areas turn out a larger number of species than the large areas.

Now, these two complementary rules admit of being explained as Darwin explains them. Small and isolated areas are rich in species relatively to the amount of population, because, as we have before seen, this population has been permitted to develop an independent history of its own, shielded from intercrossing with parent, and from struggle with exotic forms. On the other hand, large and continuous areas are favourable to the production of numerous species, first, because they contain a large population, so favouring the occurrence of numerous variations ; and, secondly, because the large area furnishes a diversity of conditions in its different parts, as to food, climate, altitude, and so forth.

Such being the state of the facts, it is obvious that physiological selection must have what may be termed a first-rate opportunity of assisting in the manufacture of species on large areas. For, not only is it upon large and continuous areas that the antagonistic effects of intercrossing are most pronounced (and, therefore, that the influence of physiological selection must be most useful in the work of species-making) ; but here also the large population, as well as the diversity in the external conditions of life which the large area supplies to different parts of that population,—both these circumstances cannot fail to furnish physiological selection with a greater abundance of that particular variation in the reproductive system on which its action depends. For all these reasons, therefore, we might have expected, upon my theory, that large and continuous areas should be good manufacturing factories of species.

Again, Mr. Darwin has shown that not only large areas, but likewise “ dominant ” genera upon those areas, are rich in species. By dominant genera he means genera represented by numerous individuals, as compared with other genera inhabiting the same area. This general rule he explains by the consideration that the qualities which first led to the form being dominant must have been useful qualities ; that these would be transmitted to the otherwise varying offspring ; and, therefore, that when these

offspring had varied sufficiently to become new species, they would still enjoy their ancestral advantages in the struggle for existence. And this, I doubt not, is in part a true explanation; but I also think that the reason why dominant genera are rich in species is chiefly because they everywhere present a great number of individuals exposed to relatively great differences in their conditions of life, or, in other words, that they furnish the best raw material for the manufacture of species by physiological selection, as explained in the last paragraph. For, if the fact of dominant genera being rich in species is to be explained *only* by natural selection, it appears to me that the useful qualities which have already led to the dominance of the ancestral type ought rather to have proved inimical to its splitting up into a number of subordinate types. If already so far "in harmony with its environment" as to have become for this reason dominant, one would suppose that there is all the more reason for its not undergoing change by the process of natural selection. Or, at least, I do not see why the fact of its being in an unusual degree of harmony with its environment should in itself constitute any unusual reason for its modification by survival of the fittest. On the other hand, as just observed, I do very plainly see why such a reason is furnished for the modifying influence of physiological selection.

Let us next turn to another of Mr. Darwin's general rules with reference to distribution. He took a great deal of trouble to collect evidence on the two following facts, namely: 1st, that "species of the larger genera in each country vary more frequently than the species of the smaller genera"; and 2nd, that "many of the species included within the larger genera resemble varieties in being very closely, but unequally, related to each other, and in having restricted ranges."* By larger genera he means genera containing many species; and he accounts for these general facts by the principle "that where many species of a genus have been formed, on an average many are still forming." But how forming? If we say by natural selection alone, we should expect to find the multitudinous species differing from one another in respect of features presenting utilitarian significance; yet this is precisely what we do not find. For Mr. Darwin's argument here consists in showing that "in large genera the amount of difference between the species is often exceedingly

* 'Origin of Species,' ed. 6. pp. 44, 45.

small, so that in this respect the species of the larger genera resemble varieties more than do the species of the smaller genera." Therefore the argument, while undoubtedly a very forcible one in favour of the fact of *evolution*, appears to me scarcely consistent with the theory of *natural selection*. On the other hand, the argument tells strongly (though unconsciously) in favour of physiological selection. For the larger a genus, or the greater the number of species it contains, the greater must be the opportunity afforded for the occurrence of that particular kind of variation on which the principle of physiological selection depends. All the species of a genus may be regarded as so many varieties which have already been separated from one another physiologically; therefore each of them may now constitute a new starting-point for a further and similar separation—particularly as, in virtue of their previous segregation, many of them are now exposed to different conditions of life. Thus, it seems to me, we can well understand why it is that genera already rich in species tend to grow still richer; while such is not the case in so great a degree with genera that are poor in species. Moreover, we can well understand that, multiplication of species being in the first instance determined by changes in the reproductive system alone, wherever a large number of new species are being turned out, the secondary differences between them should be "often exceedingly small"—a general correlation which, so far as I can see, we are not able to understand on the theory of natural selection.

The two subsidiary facts, that very closely allied species have restricted ranges, and that dominant species are rich in varieties, both seem to tell more in favour of physiological than of natural selection. For "very closely allied species" is but another name for species which scarcely differ from one another at all except in their reproductive systems; and, therefore, the more restricted their ranges, the more certainly would they have become fused by intercrossing with one another, had it not been for the barrier of sterility imposed by the primary distinction. Or rather, I should say, had it not been for the original occurrence of this barrier, these now closely-allied species would never have become species. Again, that dominant species should be rich in varieties is what might have been expected; for the greater the number of individuals in a species, the greater is the chance of variations taking place in all parts of the organic type, and particularly in the

reproductive system, seeing that this system is the most sensitive to small changes in the conditions of life, and that the greater the number of individuals composing a specific type, the more certainty there is of some of them encountering such changes. Now, of all the variations going on in all parts of the organic type, those which occur in the reproductive system of the kind required by physiological selection are most likely to be preserved, seeing that all other variations are likely to be swamped by free intercrossing. Hence, the richness of dominant species in varieties is, I believe, mainly due to the greater opportunity which such species afford of some degree of sterility arising between its constituent members.

Here is another general fact, also first noticed by Darwin, and one which he experiences some difficulty in explaining on the theory of natural selection. He says:—"In travelling from north to south over a continent, we generally meet at successive intervals with closely-allied or representative species, evidently filling the same place in the economy of the land. These representative species often meet and interlock, and as one becomes rarer and rarer, the other becomes more and more frequent, till the one replaces the other. But if we compare these species where they intermingle, they are generally as absolutely distinct from each other in every detail of structure as are specimens taken from the metropolis of each. . . . In the intermediate region, having intermediate conditions of life, why do we not now find closely-linking intermediate varieties? This difficulty for a long time quite confounded me. But I think it can in large part be explained"*.

This explanation is that, as "the neutral territory between two representative species is generally narrow in comparison with the territory proper to each, . . . and as varieties do not essentially differ from species, the same rule will probably apply to both; and, therefore, if we take a varying species inhabiting a very large area, we shall have to adapt two varieties to two large areas, and a third variety to a narrow intermediate zone." It is hence argued that this third or intermediate variety, on account of its existing in lesser numbers, will probably be soon overrun and exterminated by the larger populations on either side of it. But surely this argument overlooks one all-important fact, namely, that varieties *do* "essentially differ from species" in

* 'Origin of Species,' ed. 6, pp. 134-135.

respect of being able freely to intercross with one another. Therefore, how is it possible "to adapt two varieties to two large areas, and a third (transitional) variety to a narrow intermediate zone," in the face of free intercrossing on a continuous area? Let A, B, and C represent the three areas in question. According

A	B	C
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to the argument, variety A passes first into variety B, and then into variety C, while variety B eventually becomes exterminated by the inroads both from A and C. But how can all this have taken place with nothing to prevent intercrossing throughout the entire area A B C? I confess that to me it seems this argument can only hold on the supposition that the analogy between varieties and species extends to the reproductive system; or, in a sense more absolute than the argument has in view, that "varieties do not essentially differ from the species" which they afterwards form, but from the first showed some degree of sterility towards one another. And, if so, we have of course to do with the principles of physiological selection.

That in all such cases of species-distribution these principles have played an important part in the species-formation, appears to be rendered further probable from the suddenness of transition on the area occupied by contiguous species, as well as from the completeness of it—*i. e.* the absence of connecting forms. For all these facts combine to testify that the transition was originally due to that particular change in the reproductive systems of the forms concerned, which still enables those forms to "interlock" without intercrossing.

But this leads us to another general fact, also mentioned by Darwin, and well recognized by all naturalists, namely, that closely allied species, or species differing from one another in trivial details, usually occupy contiguous areas; or, conversely stated, that contiguity of geographical position is favourable to the appearance of species closely allied to one another. Of course this fact speaks in favour of evolution; but where the question is as to method, I confess that the theory of natural selection appears to me wholly irrelevant. For in all the numberless cases to which I allude, the points of minute detail wherein the allied species differ in respect of secondary distinctions are points

which present no utilitarian significance. And, as previously argued, it is impossible to believe that there can be any general or constant correlation between disguised utility and insignificance of secondary distinction.

Now, the large body of facts to which I here allude, but will not at present wait to specify, appear to me to constitute perhaps the strongest of all my arguments in favour of physiological selection. Take, for instance, a large continental area and follow across it a chain of species, each link of which differs from those on either side of it by the most minute and trivial distinctions of a secondary kind, but all the links of which differ from one another in respect of their reproductive systems, so that no one member of the series is perfectly fertile with any other member. Can it be supposed that in every case this constant primary distinction has been superinduced by the trivial secondary distinctions, distributed as they are over different parts of all these kindred organisms, and yet nowhere presenting any but the most trifling amount of morphological change? Or, even if we were to suppose this, we have still to meet the question, How were all these trifling changes produced in the face of free intercrossing on the continuous area? Certainly not by natural selection, seeing that they are useless to the species presenting them. Let it then be by changes in the conditions of life, whether of food, of climate, or of any thing else. I can conceive of no other alternative. Yet if we accept this alternative, we are but espousing—in a disguised and roundabout way to be sure—the theory of physiological selection. For we are thus but hypothetically assigning the causes which have induced the primary distinction in each case, or the causes which have led to the mutual sterility. For my own part, I believe that the assignation would be, in the great majority of such cases, incorrect. That is to say, for reasons already given, I do not believe that in the great majority of such cases the trivial secondary distinctions, howsoever these were caused, can have had any thing to do with the great primary distinction. What I believe is, that all the closely allied species inhabiting our supposed continent, and differing from one another in so many points of minute detail, are but so many records of one particular kind of variation having taken place in the reproductive systems of their ancestors, and so often as it did take place, having necessarily given birth to a new species. The primary distinc-

tion thus became the constant distinction, simply because it was in virtue of this distinction, or in virtue of the variation which first originated this distinction, that the species became species; and the secondary distinctions thus became multitudinous, minute, and unmeaning, simply because they were of later origin,—the result of spontaneous variability, unchecked by intercrossing with the parent forms, and, on account of their trivial (*i. e.* physiologically harmless) nature, unchecked also by natural selection, economy of growth, or any other principle which might have prevented spontaneous variability of any other kind.

RELATIONS BETWEEN SURVIVAL OF THE FITTEST AND SEGREGATION OF THE FIT.

In several preceding parts of this paper, I have had occasion to notice some of the relations between the two forms of selection, natural and physiological. But it seems desirable to consider this matter a little more closely.

First of all, it will have been observed that the theory of physiological selection in some respects resembles and in other respects differs from that of natural selection. Thus to some extent the two theories resemble one another in the kind of evidence by which they are each supported. In neither case does the theory rest upon any actual observation of the origin of species by the agency supposed; in both cases, therefore, the evidence of the agency is deduced from general considerations regarding the morphology and distribution of specific forms, as well as the observable relations in which such forms now stand to one another. Thus, in the case of each theory alike, the argument takes the form of first establishing a *prima facie* case, showing the antecedent probability of the cause in question; and next in proving, by a general survey of organic nature, that many of the facts are such as they ought to be if the theory in question is true.

So far, then, the two theories are logically similar in form; but in certain material points they widely differ.

To begin with, it is obvious that as natural selection is a theory of the origin of adaptations, it is a theory of the origin of genera, families, orders, and classes, quite as much as it is a theory of the origin of species. Indeed, as I have already given reasons to show, it appears to me that natural selection is much more a

theory of the origin of genera, families, orders, and classes, than it is a theory of the origin of species. Physiological selection, on the other hand, is almost exclusively a theory of the origin of species, seeing that it can but very rarely have had anything to do with the formation of genera, and can never have had anything at all to do with the formation of families, orders, or classes. Hence, the evidence which we have of the evolutionary influence of physiological selection, unlike that which we have of the evolutionary influence of natural selection, is confined within the limits of specific distinctions.

Again, physiological selection differs from natural selection in that the variations on the occurrence of which it depends are variations of an unuseful kind. But, if the principle acts at all, it must resemble natural selection in being quite as vigilant in the selection, and quite as potent in the formation of organic types; seeing that any variation in the reproductive system of the kind in question must be preserved by the principle in question, and this with even more certainty than are the useful variations which furnish material to the working of natural selection. For while these useful variations—especially in their incipient stages, when few in number and unpronounced in character—are obviously exposed to the most serious risk of extinction from intercrossing, there is no such risk in the case of this non-useful variation. Here the obliterating effects of intercrossing on the new variety are from the first excluded by the very fact of its being a variety, or in virtue of the very peculiarity which distinguishes it as a variety. Physiological selection therefore, has this great advantage over natural selection,—although it is confined to selecting only one kind of variation, and this only in the reproductive system, whenever this one kind of variation occurs it cannot escape the preserving agency of physiological selection. Hence, even if it be granted that the variation which affects the reproductive system in this particular way is a variation of comparatively rare occurrence, still, as it must always be preserved whenever it does occur, its influence in the manufacture of specific types must be cumulative, and, therefore, in the course of geological time, probably immense.

So much, then, for the resemblances and the differences between the two theories. It only remains to add that the two are complementary. I have already shown some of the respects in which the newer theory comes to the assistance of the older, and this in

the places where the older has stood most in need of assistance. In particular, I have shown that segregation of the fit entirely relieves survival of the fittest from the difficulty under which it has hitherto laboured of explaining why it is that sterility is so constantly found between species, while so rarely found between varieties which differ from one another even more than many species; why so many features of specific distinction are useless to the species presenting them; and why it is that incipient varieties are not obliterated by intercrossing with parent forms. Again, we have seen that physiological selection, by preventing such intercrossing, enables natural selection to promote diversity of character, and thus to evolve species in ramifying branches instead of in linear series—a work which I cannot see how natural selection could possibly perform unless thus aided by physiological selection. Moreover, we have seen that although natural selection alone could not induce sterility between allied types, yet when this sterility is given by physiological selection, the forms which present it would be favoured in the struggle for existence; and thus again the two principles are found playing, as it were, into each other's hands. And here, as elsewhere, I believe that the co-operation enables the two principles to effect very much more in the way of species-making than either of them could effect if working separately. On the one hand, without the assistance of physiological selection, natural selection would, I believe, be all but overcome by the adverse influences of free intercrossing—influences all the more potent under the very conditions which are required for the multiplication of species by divergence of character. On the other hand, without natural selection, physiological selection would be powerless to create any differences of specific type, other than those of mutual sterility and trivial details of structure, form, and colour—differences wholly without meaning from a utilitarian point of view. But in their combination these two principles appear to me able to accomplish what neither can accomplish alone—namely, a full and satisfactory explanation of the origin of species.

GENERAL SUMMARY AND CONCLUSION.

Seeing that the theory of natural selection is confessedly unable to explain the primary specific distinction of sterility, as well as a large proportional number of the secondary specific distinctions; seeing also that, even as regards the remainder, it is

difficult to see how natural selection alone could have evolved them in the presence of free intercrossing; seeing all this, it becomes obvious that natural selection is not a theory of the origin of species: it is a theory of the genesis of adaptive modifications, whether these happen to be distinctive of species only, or likewise of higher taxonomic divisions. Only, if species were always distinguishable in points of utilitarian significance, if natural selection were able fully to explain the fact of their mutual sterility, and if it were a part of the theory to show that in some way the mutual crossing of varieties is prevented; only under these circumstances could it be properly said that a theory of the genesis of adaptive modifications is likewise a theory of the origin of species. But, as matters stand, supplementary theories are required. Of these the only ones hitherto suggested are the theories of use and disuse, sexual selection, correlated variability, prolonged exposure to similar conditions of life, and prevention of intercrossing by geographical barriers, or by migration. The first three may here be neglected, as they do not touch the subject-matter of the present paper. Prolonged exposure to similar conditions of life has been shown inadequate to explain the contrast between hybrids and mongrels in respect of fertility. The prevention of intercrossing by geographical barriers and by migration has been shown adequate to account for the frequent appearance of non-adaptive specific characters. But the great distinction of sterility between species is still left unexplained. This it is that my theory of physiological selection seeks to explain. And the theory consists merely in pointing to the fact that wherever, among all the possible variations of the highly variable reproductive system, there arises towards any parent form any degree of sterility which does not extend to the varietal form, there a new species must necessarily take its origin. For, even though the varietal form continues to live on the same area as its parent form, intercrossing is prevented by the primary distinction of sterility, with the consequence of secondary distinctions subsequently arising by way of independent variability—just as happens when the barrier to intercrossing, instead of being physiological, is geographical.

It makes no essential difference to my theory whether the causes of this particular variation on the part of the reproductive system are extrinsic or intrinsic; nor does it make any difference whether the variation first occurs in a high or in a low degree.

But many reasons have been given to show that most probably, in a large majority of cases, the primary distinction has likewise been the primordial distinction, and thus became the condition to the subsequent appearance of secondary distinctions by independent variability.

Moreover, one very important reason was given to show that, in all probability, the primary distinction is not only a *condition* to the subsequent appearance of secondary distinctions, but itself the *cause* of them; for Mr. Darwin has shown that when the reproductive system undergoes any variation, the consequences to progeny are apt to consist in variations affecting other parts of the organism. So that the prevention of intercrossing by physiological barriers differs from such prevention by geographical barriers, or by migration, in that, over and above the influence of independent variability, there is a direct causal connection between the agency which prevents intercrossing and the subsequent production of secondary specific characters.

Nevertheless, reasons have also been given to show that, in a small minority of cases, this historical order may have been reversed—the primary distinction having been superinduced by the secondary, as we sometimes (though very rarely) find to have been the case with our domesticated varieties, but which we usually find to have been the case with genera, &c. Even, however, when such has been the case with natural varieties living on the same area, it is the principles of physiological selection that have determined the result; for it can only have been those secondary distinctions which happened to have been able to induce the primary distinction that were, for this reason, allowed to survive. Thus in all cases where the evolution of species has not been due to the prevention of intercrossing by geographical barriers or by migration, it has probably been due to such prevention by the principles of physiological selection. Or, otherwise stated, all specific types which now display any degree of sterility towards allied types, are probably so many records of the particular variation with which we are concerned having arisen in the reproductive systems of their ancestry. For, not only has it been shown, on antecedent grounds, that the occurrence of this particular variation is in the highest degree probable, but it has also been shown that, as a matter of actual observation, it does occur in individuals, in varieties, and in species. Indeed, as regards species, the argument here resolved itself into a mere

statement of fact, namely, that all natural varieties which have not been otherwise prevented from intercrossing, and which have been allowed to survive long enough to develop any differences worth mentioning, are now found to be protected from intercrossing by the bar of sterility—that is, by a previous change or variation in the reproductive system of the kind which my theory requires. In many cases, no doubt, this particular change, or variation, has been caused by the season of flowering or of pairing having been either advanced or retarded in a section of a species, or to sundry other influences of an extrinsic kind; but probably in a still greater number of cases it has been due to what I have called intrinsic causes, or to the “spontaneous” variability of the reproductive system itself. In order to show how large a part the principles thus explained have probably played in the evolution of species, many arguments, which it would be tedious again to enumerate, have been drawn from the inutility of so large a proportion of secondary specific distinctions, from the swamping effects of intercrossing in the absence of physiological barriers, from the multiplication of species, and from the leading or most general facts of geographical distribution. Lastly, the relations between natural and physiological selection have been shown to be co-operative, the latter allowing the former to act by interposing its laws of sterility, with the result that secondary specific distinctions may be either adaptive or non-adaptive in character. On the other hand, natural selection may assist physiological selection by setting a premium both on the primary and on the secondary distinctions—*i e.* encouraging the work both of sterilizing species and of diversifying their characters.

In conclusion, therefore, it seems to me almost impossible to doubt, when so many large and general facts combine in pointing to the principles of physiological selection, that these principles must be accredited with a highly important share in the evolution of species. Mr. Darwin has well said, “From the laws governing the various grades of sterility being so uniform throughout the animal and vegetable kingdoms, we may infer that the cause, whatever it may be, is the same, or nearly the same, in all cases.” This cause, as he candidly shows in the paragraphs from which the quotation is made *, obviously cannot have been natural selection. But to my mind it appears no less obvious that the

* ‘Origin of Species,’ ed. 6. p. 248.

cause in question is the cause which I have termed physiological selection. For what are the effects which stand to be explained? Broadly stated, these effects are simply millions and millions of cases where there is a constant association between secondary specific characters, whether useful or unuseful, and the primary specific characters of sterility with allied forms. Be it observed that all these innumerable cases are alike in *kind*, however much they may differ in regard to the *degree* of sterility. In a considerable proportion of cases there is no sterility at all, and from this zero level we encounter all degrees of it, until we reach the maximum degree, where sterility is absolute.

Now, we have seen that these differences are exactly what my theory requires. For, 1st, in a considerable proportion of cases intercrossing has been prevented by geographical barriers and by migration; in these cases, therefore, physiological selection has had nothing to do with the evolution of species, which thus continue, as we might have expected, fertile *inter se*. 2nd, in many other cases physiological selection must have been assisted in its work of preventing intercrossing, whether by partial barriers of a geographical kind, partial migrations, slight changes of climate, habitat, instinct, and so forth; in these cases, therefore, the resulting species now continue to manifest corresponding fertility between themselves, or fertility in all degrees. Hence, if sterility between allied species were always absolute, or even always considerable, the fact would be fatal to my theory; for this would show that sterility between allied forms must have been due to some cause other than the mere, but necessary, preservation of one particular kind of variation, whenever it happens to arise. But, as matters actually stand, we are able to explain the absence of sterility by the absence of physiological selection, and the presence of different degrees of sterility by the presence of different degrees of such selection.

Confining, then, our attention to that large proportional number of cases where the association in question obtains, and disregarding the different degrees of sterility, what really stands to be explained is the great and general fact of the association itself. For what does this fact imply? It implies that (the now explained exceptions apart), so soon as natural varieties become entitled to take rank as species, they are found to be varieties which, however much they may differ in other or secondary dis-

tinctions, agree in presenting the constant distinction in respect of their reproductive systems. In other words, systematists, in their classification of species, have always been engaged in unconsciously tabulating the records of cases where overwhelming intercrossing with parent forms has been prevented; and the only way in which we can account for the now very frequent occurrence of sterility between allied species is by supposing that in these cases it was this sterility which prevented the intercrossing, or constituted the condition to these species being formed. It serves still further to enforce this view of the case when we try to imagine what would happen if the now existing sterility between all allied species which present it were suddenly removed. In this case free intercrossing within the limits of each genus would soon reduce all specific types living on common areas to as small a number of species as there are now genera. But if this is what would certainly be the result on all common areas if the physiological conditions now existing were removed, must we not conclude that it was owing to the fact of these conditions that the now existing species arose?

Or, again, let us contrast the difference between natural species and domesticated varieties. These, as we have seen, resemble each other in every respect save in the one respect of mutual sterility. Can we, therefore, doubt that this condition, so often as it occurs, has played the same part in the evolution of natural species as the prevention of intercrossing by artificial barriers has played in the evolution of domesticated varieties? Or can we doubt that if intercrossing were in any other way prevented, natural species would resemble domesticated varieties still more closely in presenting well-marked differences of type without this peculiar association with the barrier of sterility? But if any one should doubt this, we have only to point to the unquestionable fact, that where intercrossing has been otherwise prevented—whether by geographical barriers or by migration—such well-marked differences of type have arisen, though in these cases they are not necessarily associated with the physiological barrier in question. Therefore, when this barrier is present, how can it be reasonable to doubt that its connection with the other differences of type is a connection of casuality? For does not this extraordinarily general connection prove that it is only those cases of variation in any other part of any organism which happen to have been associated with the physiological barrier of sterility that have

been able to survive under all circumstances where they would have otherwise inevitably perished by free intercrossing?

Looking to the very general association on which I am dwelling, I cannot wonder that in the pre-Darwinian days naturalists were led to suppose that the primary distinction of sterility was divinely accorded to species, for the purpose of preventing their secondary distinctions from becoming lost by intercrossing. And I cannot help feeling that these naturalists were less blind than their successors; for at least they had an intelligible theory whereby to explain the general association which we are considering, whereas their successors have absolutely no theory at all. They are, therefore, much in the same position as a man might be who wonders at the constant association between a flowing river and a continuously descending excavation; for in both cases the association is much too frequent and general to be accounted for by chance, so that, if it is not to be accounted for by design, there only remains the alternative of accounting for it by a connection of casuality. Yet, naturalists are now in the same state of mind as the man above supposed; they merely wonder at the association without perceiving its obvious import. For, assuredly, it is quite as obvious that species could not exist as species without the physiological condition of sterility, as it is that a river could not exist as a river without the physical condition of declivity. And just as in the latter case, wherever the requisite physical conditions occur, streams and rivers come into existence by way of natural consequence, so in the former case, wherever the requisite physiological conditions occur, species and genera arise as a no less inevitable result.

It only remains to be said that the theory of physiological selection has this immense advantage over every other theory that has ever been propounded on the origin of species: it admits of being either demonstrated or destroyed by verification. But the process of verification will be a most laborious one, and cannot be satisfactorily completed (even if many naturalists should engage upon it) without the expenditure of years of methodical research. In view of this consideration, I have deemed it best to publish my theory before undertaking the labour of verification; for, by so doing, I hope to induce other naturalists to co-operate with me in carrying on the research in different parts of the world. With this object, I will conclude by briefly

sketching out the lines on which the work of verification may proceed.

There are two main branches of testing inquiry, the one experimental, and the other systematic. It is open to the systematist, in any department either of botany or zoology, to utilize his knowledge as a specialist in the following way. Let him cast about for closely allied species which are thoroughly well separated from one another, either by geographical barriers or by migration. When he has found any two closely allied species which, for either of these reasons, he feels justified in certainly concluding can never have had an opportunity of intercrossing, let him ascertain whether they are not fertile with one another. The species ought to be as closely allied as possible, because, if they differ in any considerable degree, even though the distinction between them is nominally specific, it really approaches a distinction that is generic; and in the case of genera there is no question as to sterility being due to a general difference of organic type. Moreover, the specialist ought not to rest satisfied with only a few observations. His aim ought rather to be to make his observations over a large number of species, tabulate the results, and then see whether the average amount of sterility yielded by all his selected species is not considerably lower than a similar average obtained by selecting a similar number of closely allied species now inhabiting the same continuous area—taking care, however, to choose areas which are believed to have been continuous for long periods of time. Perhaps the best rule to follow (especially in the case of plants) would be to take species which are peculiar to oceanic islands, and to match these with allied species on mainlands, for the first set of tables; while, for the second set, allied species, both of which are peculiar to the same large continental area, should be chosen. If these observations were made over a considerable number of cases, I should expect them to show an unmistakable difference in the results of the two sets of averages. But it would be necessary to make them over a considerable number of cases, because by this method of inquiry we could never be sure that all modifying conditions had been excluded. Even if we could know the life-histories of each species chosen, there would still remain the element of doubt which is incidentally mentioned by Mr. Darwin in another connection—namely, that “if a species was rendered sterile with some one compatriot, sterility with other species would (? might)

follow as a necessary contingency." So that, in view of these considerations, I am disposed to think that even wholly negative results yielded by this branch of inquiry would not be absolutely fatal to my theory, although, no doubt, most damaging to its probability.

The other branch of inquiry consists in looking out for cases of two well-marked natural varieties living together on the same area, and ascertaining by experiment whether these are not more fertile within their own limits than they are with one another. Plants would lend themselves to these experiments much more readily than animals; and in the case of plants the experiments would not be very difficult to try, while the results when obtained would be less open to doubt than those obtainable by the method above mentioned. I therefore hope that botanists in different parts of the world will deem it worth their while to see whether it is not possible to gain this direct evidence, at once of evolution as a fact, and of physiological selection as a method.

The points to be attended to in conducting these experiments are as follows.

Let the varieties be well marked, or, at least, constant within themselves; let there be no question that both the varieties are endemic as well as common to the area which they occupy. In conducting the experiments care should be taken not to disturb the natural conditions of the individuals chosen, whether by transplantation or in any other way. And, of course, it is needless to add that not only care must be taken, but certainty secured, that the only source of fertilization of the individuals chosen is that of the pollen used by the observer. The experiments, which ought to be conducted over a large number of individuals, will in every case divide themselves into four sets:—1st, fertilization of A by B; 2nd, fertilization of B by A; 3rd, of A by A; and 4th, of B by B; where A and B are the two varieties in question. In every one experiment of these four sets of experiments the seed which is yielded must be counted and sown. When all the experiments are over, let it thus be ascertained whether there is any difference in the *degrees* of fertility which have been yielded by experiments 1 and 2, and by 3 and 4 respectively.

POSTSCRIPT.

In the discussion which followed the reading of this paper, certain difficulties or objections were put forward by one or two of the more eminent naturalists who happened to be present. These I answered verbally; but, inasmuch as they may also occur to readers of the paper, I will here briefly consider those among them which do not appear to have been sufficiently anticipated in the course of the preceding pages.

First, it was objected that breeding in and in has a tendency to deteriorate offspring, and therefore that physiological selection, by limiting the area of breeding, would yield a variety less able than its parent form to compete successfully in the struggle for existence. This objection, however, would only be of any force where an exceedingly small number of individuals are concerned; and even then, I think, it may be neglected, seeing that in the course of a very few generations consanguinity becomes diluted in so rapid a ratio, even in the case of species which produce but few at a birth. On this point I may refer to the 'Origin of Species,' pp. 72, 238, and 252, to show that even Mr. Darwin (who more than any other writer has insisted on the benefit arising from cross-fertilization) disregards the effects of interbreeding, where more than a very few individuals are concerned.

Next, it was objected that it could be of no *use* to a varietal type that it should be separated from the parental. I have, however, argued that the use would be three-fold: 1st, the variety would thus be started on an independent course of history; 2nd, it would therefore be able "to seize on many and widely diversified places in the economy of nature;" and, 3rd, it would derive the advantage that breeders find in keeping their strains from intercrossing. But, over and above all this, the theory of physiological selection does not require that the separation in question should be of any use; and, therefore, this objection to the theory falls to the ground as irrelevant. So long as there is no actual *detriment* arising to the variety on account of its being separated from the parent, any ideas derived from the theory of natural selection are plainly without bearing upon the subject.

Lastly, it was in effect suggested that the theory of physiological selection is merely the re-statement of a fact. For,

as I have myself argued (pp. 361, 399-400), upon the general theory of evolution it must be accepted as a fact that, so soon as varieties have diverged from their parental type sufficiently far to take rank as species, some such change in the reproductive system as that of sterility with allied forms has usually been found to have occurred. Now, it is perfectly true that this is the well-known fact, and, moreover, as I have previously endeavoured to insist, that it is the fact which more than any other stands to be explained by any theory of the origin of species. But, obviously, the theory of physiological selection is something more than a mere re-statement of this fact: it is an *explanation* of the fact in terms of evolutionary philosophy.

First, let it be observed that the supposed objection is not concerned with any question touching the validity of the evidence adduced to show that the particular kind of variation on which my theory depends does actually take place; nor is the objection concerned with any doubt as to the extent in which this variation may have operated in the origination of species. On the contrary, the objection goes upon the ground of accepting all the evidence which I have adduced upon these points, and then representing that, granting it all, it merely amounts to a re-statement of fact. Well, let the evidence be granted, and, therefore, let it be assumed that the majority of natural species are so many records of a particular kind of variation having taken place in the reproductive systems of ancestors. The issue then resolves itself into the question whether this is a mere re-statement of fact, or whether it serves to throw any new light in the way of explanation.

By an explanation I understand the pointing out of effects as due to the operation of causes. In the present instance, the effect which has to be explained is the differentiation of specific types. This I have sought to do by invoking the agency of a well-known event—viz., that of variation—and showing that whenever this cause affects the reproductive system in a particular way, a new species must arise as an effect. Now, I believe that this mode of viewing the problem as to the origin of species is not only new, but, if true, serves to solve the problem, or to explain the facts. The facts, indeed, were there before, as must always be the case before an explanation can be suggested; but an explanation consists in placing the facts in a certain relation to one another—*i. e.* in a relation of proved causality. In the present instance

this, so far as I am aware, has not been previously done. The facts of variation have been known, and the facts of specific sterility have been known; but hitherto it has not been suggested that the former may stand to the latter in the relation of cause to effect, or that when a particular kind of variation occurs in the reproductive system a new species must necessarily ensue. The very general association between mutual sterility and specific differences of other kinds has, indeed, forced itself upon the attention of naturalists; but naturalists have attempted to explain the association by this, that, and the other collateral cause, such as divine interposition, uniform conditions of life, and so forth. The present theory, on the other hand, seeks to explain this association as itself an association of cause and effect; the theory regards a species as nothing more than a variety, where the variation happens to have affected the reproductive system in a particular way—thus leading to physiological separation, and so eventually to other morphological changes, as previously argued. Now, whatever may be thought as to the probability of this explanation, to me it appears evident that it is an explanation, and not merely a re-statement of fact. For, if not, where has been the need of all that has been written for the purpose of endeavouring to explain the association? If it has ever before been recognized that species are the effects of variations in the reproductive systems of ancestry, I cannot understand why this should not have been clearly stated; and still less can I understand why, with so simple an explanation before the mind, any naturalist should have cast about for other causes of a collateral kind. What I can understand is that more evidence should be demanded of the truth of the present explanation; but this is not the point with which the objection before us is concerned.

The real standing of the matter is simply this. Evolutionists have hitherto regarded mutual sterility as one among the effects of specific differentiation, and they have therefore been led to seek for causes which might be held adequate to account for this effect. My theory, on the other hand, regards the sterility, wherever it occurs, as itself the cause of specific differentiation; and this whether the sterility be spontaneous or induced by changes going on in other parts of the organism, as previously explained. Evolutionists have hitherto failed to find the causes of which they have been in search; and, according to my view, necessarily so, inasmuch as there are no such causes to be found.

The association between specific divergence and mutual sterility has therefore appeared, in a high degree, inexplicable; so that, in Mr. Darwin's words, "the real difficulty" presented to evolutionists has been to explain why mutual sterility "has so generally occurred with natural varieties, as soon as they have been permanently modified in a sufficient degree to take rank as species"—a difficulty which he thought we were still far from solving, inasmuch as "we are far from precisely knowing the cause." But the whole of this apparently great and inexplicable difficulty has arisen on account of regarding the sterility as, in some way or another, the *consequence* of a natural variety becoming "permanently modified." Once let the point of view be changed, or once let us see in the sterility the *antecedent* of the permanent modification, and, as it appears to me, there is an end of the matter: "the real difficulty" has vanished, seeing that we are no longer "far from precisely knowing the cause" of the general association between sterility and divergence. But, if so, can it be said that the solution of such a problem, the removal of such a difficulty, or the pointing out of such a causal relation, is nothing more than a re-statement of fact? Yet this is what the objection which I am considering amounts to; for, as previously remarked, it goes upon the ground of accepting my whole argument, and questions only the character of that argument as an explanation.

It may serve to place this matter in a still clearer light if I briefly indicate one important consequence of my suggested explanation of the origin of species, and one which certainly could not arise if this explanation were nothing more than a re-statement of facts already recognized. Hitherto it has been the aim, or argumentative bias, of evolutionists to disparage—and even to ignore—the swamping influence of intercrossing; for, according to the supposition that sterility of species is an effect of morphological divergence, it obviously follows that this swamping influence of intercrossing must be held inimical to such divergence, or to the formation of new species. According to my view, on the other hand, it is just this swamping influence of intercrossing that constitutes the *raison d'être* of all species which present any degree of sterility with allied forms. For, according to my view, it is only this one particular variation in the way of such sterility which, being in virtue of its own character shielded from the swamping influence, is for this reason allowed to survive: it is the one particular variation that is

selected to constitute a new species. Intercrossing is thus regarded as standing in the same kind of relation to the genesis of species as the struggle for existence stands to that of adaptive structures: it is the destroying tendency which furnishes the needful condition to a selective process: it is the agency which obliterates all other variations, save those of a particular kind. Therefore, according to my theory of the origin of species, the greater the swamping influence of intercrossing the better must be the conditions for evolving species mutually sterile with one another; while, as we have seen, precisely the opposite consequence follows from all previous theories upon this subject.

Probably more than enough has now been said to dispose of the criticism which I am considering, or to show that the theory of physiological selection offers a real explanation of the origin of species, and does so by going to work at the very root of the problem. I will therefore only add that the real idea in the minds of those who advanced this criticism must, it appears to me, have been that my suggested explanation of the origin of species opens up another and a more ultimate problem—namely, granting that species have originated in the way supposed, what have been the causes of the particular kind of variation in the reproductive system which the theory requires? This, of course, is a perfectly intelligible question, and one that must immediately suggest itself to the mind: my failure to meet it is therefore apt to give rise to the impression that my theory is imperfect. But, as briefly stated in the paper itself, this question is really not one with which the theory of physiological selection can properly be regarded as having anything to do. This theory has only to take the facts of variation in general as granted, and then to construct out of them its suggested explanation of the origin of species. No doubt it would be most interesting to discover the causes of every variation that constitutes the beginning of a new specific character; but our inability to do this does not invalidate the theory of physiological selection, any more than it does the theory of natural selection. Objections, indeed, have been raised against the theory of natural selection on this very ground—namely, that it does not explain the causes of those variations on the occurrence of which it depends. But these objections are clearly illogical. It constitutes no part of the theory of natural selection to explain these variations; this is a problem which belongs to the future of physiology, and no doubt

we shall have long to wait before we derive much light upon it. But it is enough for the explanation which is furnished by Mr. Darwin's theory of the evolution of adaptive structures by natural selection, that the variations in question take place; and similarly as to the present theory of the evolution of species by physiological selection.

Whatever, therefore, may be thought as to the truth of this theory, or as to the extent of its applicability, it is certainly something very much more than a bare re-statement of fact. If the evidence which I have presented on these points is accepted (as it must be by the criticism with which I am dealing), the explanatory value of the theory may be estimated by the consideration that what Mr. Darwin has called the "mystery of mysteries"* ceases to be mysterious in any other sense or degree than the general fact that offspring do not always and in every respect resemble their parents. The birth of a new species becomes, for instance, less mysterious than the birth of a child with six toes, inasmuch as the variation which it implies is one of less departure from the specific type. Nay, it becomes even less mysterious than the occurrence of what I have termed individual incompatibility—a variation which, on account of its apparently trivial character, Mr. Darwin apologizes for so much as mentioning. Hence, unless it be denied that the clearing up of a mystery constitutes an explanation, the present theory is unquestionably an explanation of the only phenomena with which it is concerned. Although it makes no attempt at explaining the physiological causes which underlie the phenomena of variation in general, if the evidence which has been given be accepted, the theory does furnish a real explanation of the origin of species, by proving that there is one particular variation which, so often as it has taken place, must necessarily have constituted the originating cause of a new specific form.

* Viz.—the problem of the origin of species, which, as shown in the preceding paper, his theory of natural selection serves only in small part to explain.